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BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 84, NO. 4, pp. 229–236 JULY, 1957

A STUDY OF THE TUNICA CORPUS AND ANNEAU INITIAL OF IRRADIATED AND NORMAL STEM APICES OF NICOTIANA TABACUM L.[1, 2]

LAWRENCE J. CROCKETT

Work done in the past on the stem apices points to the fact that the Angiospermae, certainly the Dicotyledonae, are probably best described in terms of the Tunica-corpus theory first suggested by Schmidt (1924). In a modern review of this problem Gifford (1954) states the general usefulness of this theory for stem tip delineations and outlines with care the major concepts within the theory: stem apices are capped by one or more tunica layers; under these is found a mass of cells, less regular in their division pattern than the tunica, the corpus. The tunica layer divides only anticlinally or predominantly so. The first tunica layer divides only anticlinally; if there are several tunica layers those beneath the first divide predominantly anticlinally, but may show periclinally oriented division when certain organs are being initiated at the apex, e.g., leaves. The corpus divides in a variety of planes. Esau (1953) has stated similar facts for this concept. Plantefol (1947) adds to this general theory by stating that a region taking both tunica and corpus, at the outer portion of the tip dome may be considered as a ring of initiation, an "anneau initial". Irradiation of plant material, though not new, considering the fundamental researches with x-rays of Gager (1908), has recently become a useful tool in analyzing various aspects of growth and metabolism in plants. In this study irradiation has been applied in an attempt to understand morphogenetic expression at the stem apex of the tobacco plant (*Nicotiana tabacum* L. variety "Turkish").

The present results were obtained during the course of a morphological study of phenomena other than those herein discussed occurring at the apex of the stem. Those results will be published later.

Materials and methods. Plants of *Nicotiana tabacum* L. were grown from seeds in the greenhouses of Columbia University.[3] When they had attained a height of about five inches they were taken in their pots to the

[1] It is a pleasure to acknowledge the stimulating suggestions and advice of Professor E. B. Matzke throughout the course of this investigation.

[2] This study was partly carried out in the Department of Biology, Brookhaven National Laboratory where the author is a research collaborator. The generous and helpful cooperation of Drs. A. H. Sparrow and H. J. Curtis, and Mr. L. A. Schairer of the Department of Biology, Brookhaven National Laboratory is warmly appreciated.

[3] The instruction and assistance in horticultural techniques given on numerous occasions to the author by Mr. Steve Dobzenski, Chief Gardener, Columbia University, is deeply appreciated.

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greenhouses of the Brookhaven National Laboratory, New York. Every effort was made to keep all the plants under similar growth conditions and only those plants of approximately equal proportions and vigor were selected for the study. About half those plants taken were placed in the Co^{60} gamma irradiation greenhouse where they were exposed to gamma radiation 20 hours each day, and the other half was placed in the "normal" greenhouse close by. The strength of the Co^{60} source at this time was approximately 10.5 curies. Chronic irradation was used in this study rather than acute dosages, as chronic irradation was observed by Gunckel and Sparrow (1954) to produce more severe and varied morphological effect than acute irradiation. Apices from plants giving results in this particular study received approximately 80 r per day for 14 days and were six feet from the Co^{60} gamma source. Normal and irradiated apices were then removed and immediately killed and fixed in CRAF II. They were run through an alcohol-xylol series and embedded in paraffin. The tips were stained in safranin-aniline blue. The results of this investigation were based upon the observations upon 100 non-irradiated or normal stem apices and 30 irradiated stem tips of *Nicotiana tabacum* L. variety "Turkish". The material was sectioned at 50 micra.

Observations. Normal stem apices. In the mature stem apex of *Nicotiana tabacum* L. there are two tunica layers and a corpus beneath these, at the growth stage at which these plant's apices were fixed. The first tunica is continuous with the epidermis of newly generated leaves. In the normal plant division in this layer is in an anticlinal plane only. In this study a periclinal division was never found in the first tunica layer. The second tunica layer divides predominantly by anticlinal division, but it divides periclinally in the region of the "anneau initial" at the commencement of the initiation of new leaf primordia.

Beneath the tunica layers is the corpus. The cells of this region divide in various planes.

Thus the stem apex of *N. tabacum* L. fits the overall, general pattern of tunica-corpus. However, the manner in which the tip invariably takes the stains used in the investigation demonstrates that the pattern is not as clearly cut morphologically as that. The aniline blue is taken up by the cells of the tip in such a way that the blue color pattern of the tip conforms with the "anneau initial" concept as suggested by Plantefol (1947). Regions on either side of the tip, exactly in the position of the "anneau", are visible through a distinct difference in color pattern. The stain in these regions is clearly not as deeply taken up by the walls. The color difference is discernible in both tunica layers and in the corpus beneath them.

Between these regions lie the more centrally disposed cells of both tunica layers and the central corpus. These cells demonstrate a darker wall structure. The wall here has taken up more stain and appears thicker. The

general areas in which these features are to be found in this plant are delineated in figure 1.

At no time can a periclinal division be made out in the first tunica layer of normal tobacco plants. The general appearance of both tunica layers, by both observation and camera-lucida drawings, is of a regular nature, suggesting a row of teeth (tunica 1) or the first two layers of bricks in a wall (tunica 1 and 2). This can be seen in figure 2.

Irradiated stem apices. Irradiated apices of *N. tabacum* L. exposed to 80 r per day for 14 days at six feet from the Co^{60} gamma irradiation source showed certain variations from the normal stem apex pattern as given above. From figure 3 it can be seen that the irradiated apex, when compared

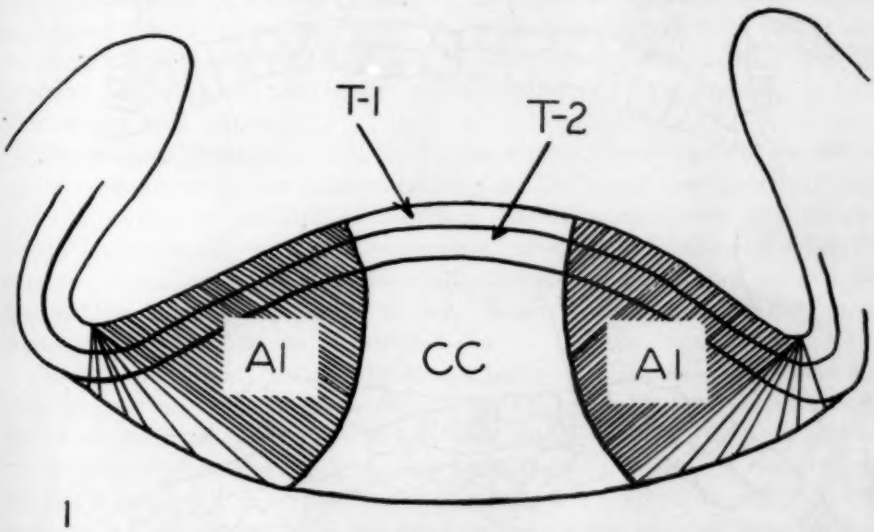

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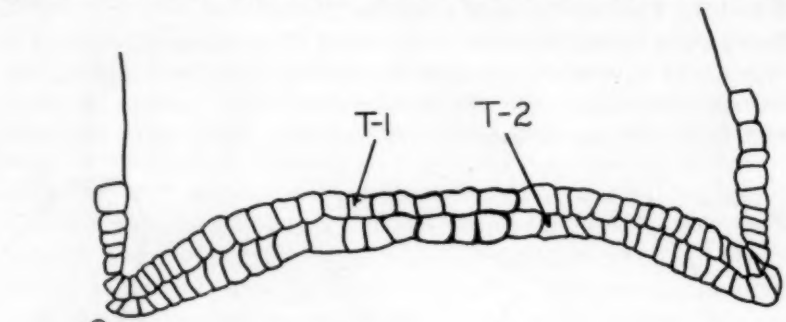
FIG. 1. Diagram of the shoot apex of *Nicotiana tabacum* L. variety "Turkish" showing regions (T-1) the first tunica layer, (T-2) second tunica layer, (CC) central corpus, (AI) anneau initial, including both portion of corpus and both layers of tunica. ×450.

with a normal tip at approximately the same stage of leaf initiation, differs in general outline. The normal tip has a more gentle arch, and is less bulged in appearance. The irradiated tip, however, demonstrates a generative region which is more raised and arches somewhat squarely; the portion of the tunica 1 layer which is within the anneau initial parallels for a short distance the vertical epidermis of the leaf being initiated, giving the apex a raised appearance.

The first tunica layer, which apparently does not divide periclinally (even during organ initiation) in normal tips, demonstrates periclinally oriented division when under irradiation (figure 3.) Such divisions apparently take place in the more centrally disposed cells of the first tunica,

and they apparently do not occur in the cells of the first tunica layer which lie well within the anneau initial. Not only are they found with relative constancy in each successive slide of tips studied, but since this material was sectioned relatively thickly, they could be discerned in focusing up and down through the section, so that it can be further said that many occur in the central portion of the apex dome. The appearance of periclinal



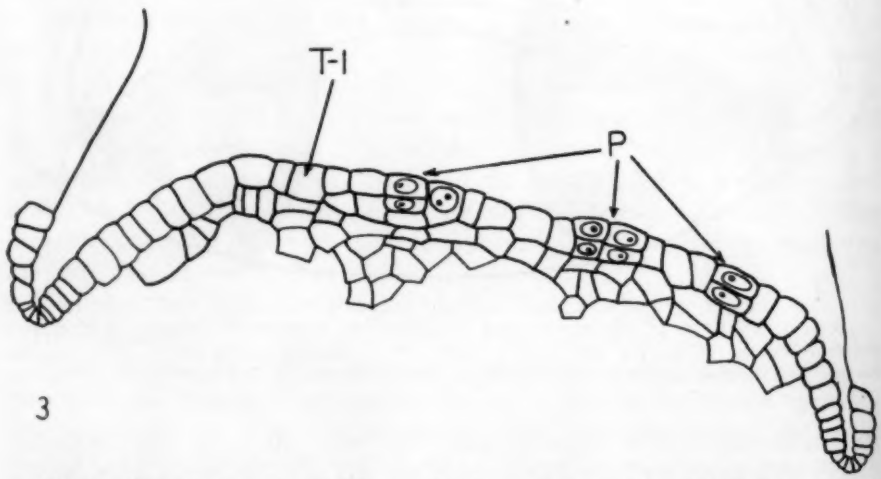


FIG. 2. Normal stem tip of tobacco showing arrangement of the first two tunica layers, (T-1) and (T-2). ×450.

FIG. 3. Irradiated stem apex of tobacco plant showing (T-1) first tunica layer, (P) periclinal divisions within the first tunica layer, (T-2) no longer a discrete layer. Anticlinal divisions still dominate the first tunica layer in the region of the anneau initial. ×450.

divisions in the first tunica layer seems to be a general phenomena under these particular conditions.

At no time in either normal or irradiated tips has a mitotic figure been observed. Considering the relatively large number of tips looked at and the thickness of the sections, this is somewhat unexpected. However, all

tips were cut and fixed at approximately 9:30 A.M. (on different occasions) when the Co^{60} source was safely down. However, from the position of the cells which had periclinally divided there could be no doubt of the periclinal nature of the divisions.

The second tunica layer in irradiated tips apparently becomes completely disorganized as a discrete layer. What in normal stem apices is a completely organized cellular layer is, in the irradiated apex, all but obliterated as a discrete layer. Even within the region of the anneau, unlike the first tunica layer, the second tunica layer loses its individuality and the corpus here appears to continue unbroken right from the first tunica layer.

The corpus though not evenly organized in normal tips because of the varied nature of the division planes of its cells, has an even more chaotic appearance in the irradiated tips. The overall, regularly and evenly arranged tooth-like pattern of the two tunicas in normal stem tips (fig. 2) is very badly interfered with; almost all regularity of arrangement is lost. This can be seen in figure 3.

Discussion. Schmidt's (1924) Tunica-corpus theory permits a much wider range of stem apex interpretation than the major theory of interpretation preceding it, viz., that of Hanstein. The Hanstein theory (1868) was revolutionary at the time of its promulgation and did establish a "layer" concept. However, it failed in its ability for adaptiveness and its general narrowness. The Tunica-corpus theory, though essentially a "layer" concept, is more plastic in its interpretations.

In this investigation the first tunica layer of *N. tabacum* L. was constantly observed to have given rise to the epidermis of new leaves. Other investigators have previously noted this under the old terminology of "dermatogen" (Avery 1933). In the Dicotyledonae there are usually two tunica layers with a corpus beneath (Gifford 1954). This applies to a majority of the species thus far studied by various authors. The present study indicates that the stem apex of *N. tabacum* L. is organized in this pattern, viz., the possession of two tunica layers and a corpus beneath.

That normal function and growth have been disturbed by irradiation with Co^{60} emitted gamma rays can be seen at a glance in comparing slides of normal and irradiated tips even under low power. That periclinal divisions, however, should be found in the first tunica layer in a normally anticlinally dividing layer is relatively surprising. This represents an apparent change of function of the layer. The normal function appears to be the generating of the epidermal layer by anticlinal divisions and the generating of more first tunica cells. The appearance of periclinals divorces the layer from a purely epidermal generating function. A layer normally producing epidermis, then, has been made to supply cells to the more central corpus. The third tunica layer of *Coleus blumei* divides both anticlinally and periclinally in normal plants (Holtzmann 1951). The abnormal, irradiated first tunica of *N. tabacum* L. then, has been made to assume a

function similar to the third tunica of *Coleus blumei*, especially in the centrally placed cells. The anticlinal pattern of division is maintained, in general, in the region of the anneau initial.

The fact that the first tunica layer maintains its anticlinal division pattern in the region of the anneau initial is another interesting feature and worthy of consideration. Not only does it mark the anneau initial as a region of difference, as staining shows it to be, but it demonstrates that this region is more resistant to change by irradiation at least in this respect.

The obvious stain-take difference at the stem apex of the plant used in this study further highlights the difference. The normal plant has a tip which takes the stain in such a way that the pattern at the tip and the anneau initial of Plantefol (1947) as shown in figures in his paper establishing the idea, are comparable. Definite regions of stain-take are plainly seen. This difference is very likely a physiological one due fundamentally to the difference in cell activity of the various regions of the stem apex. The cells of the anneau initial are apparently more active than those of the central area. It is above the anneau that the leaf buttresses first make their appearance. The walls of these cells stain less deeply; they are thinner, and this suggests that they are more active and are capable of physiological activity which is different from that in the more centrally placed cells. Though no measurements have been made for this study, they appear to be smaller cells.

The central cells, those of the tunica layers and those of the central corpus have thicker walls. At this stage in their development they look larger and do not give the suggestion of physiological activity characteristic of those of the anneau initial. In general the very central cells of the first tunica are larger horizontally than the cells of this layer found at the outer region of the tip dome. They give the appearance of more inert cells. The central cells of the corpus immediately below the first two layers of tunica cells also stain differently and look as though they may differ physiologically as well. Such a region of possible inactivity has already been suggested by Buvat (1952, 1953). This region he designated the "meristeme d'attente", and this coincides with the observed region of greater stain uptake at the apex of the plants used for this study. Buvat's "meristeme d'attente" includes most of the central portion of the second tunica and those cells of about one half the corpus lying just under the second tunica layer. That periclinal divisions should occur in the first tunica in the region above this particular portion of the corpus further suggests that the region may be different in fundamental ways from the anneau initial.

Perhaps, as Buvat (1952, 1953) suggests, this is a region of less activity. Apparently the cells are more vacuolate; they seem to have thicker walls. In addition the central cells of the tunica layers have longer axes in the horizontal, which makes them different in shape from those within the

region of the anneau initial. Probably they are not dividing with the frequency of their counterparts in the anneau initial either. It is frequently observed that the upper wall surface of the central tip dome is undulate or shows a crinkled surface. This seems to suggest that these cells are not involved in much of the activity of the tip. A further investigation of this aspect of normal stem apices is planned.

Only one observation does not agree with the fact that the anneau initial apparently takes irradiation with less damage than the more centrally placed cells. The second tunica layer even wthin the anneau initial is, in slide after slide, no longer apparent as a definite cellular layer. This layer, dividing predominantly anticlinally in normal tissue, loses its discreteness as a layer within the anneau initial. These facts indicate a disturbance of polarity: a layer dividing purely anticlinally, now shows periclinal division; another layer, discrete at first and dividing only anticlinally melts into the corpus. This certainly suggests a change of polarity at the stem apex.

Further, the possibility exists that the second tunica layer, which undergoes periclinal divisions within the anneau during normal leaf initiation, is more easily influenced by gamma irradiation effect than is the first tunica which undergoes no periclinally oriented divisions at any time during normal or undisturbed growth.

Such results however, do indicate that the zones usually designated tunica and corpus are interdependent. They apparently act together in the anneau initial of normal plants. In irradiated plants the first tunica may even contribute cells to the regions beneath, thus acting as deeper layers usually do. But this then shows that there is evidently a difference in parts of the tunica and corpus within the area of the tip dome; that the layers are different in parts. This could be interpreted to weaken the whole idea of tunica-corpus, only that right from the very beginning the theory allowed for such interpretations. The appearance of periclinal divisions within the first tunica in this study is a striking result. Is this, perhaps, the demonstration of a reversion, under adverse conditions, in which the first cellular layers contributed to the entire tip? Or is it self preservation on the part of the plant, since heavy irradiation of tips tend to burn out the most central part. The appearance of periclinal divisions may represent a response to maintain the central layers as the effect of irradiation becomes more severe for the apex.

The more raised appearance of the irradiated stem apex could occur if the timing of leaf buttress appearance was disturbed. This very likely does occur. The area of leaf appearance would be raised as it is in figure 3, if the central cells of the apex were to divide (especially periclinally) and leaf appearance was slowed down. Then the surface layers could be relatively continuous while the dome would develop relatively parallel and low, raised sides in the region of the anneau as it does in figure 3.

SUMMARY

1. The stem apices of *Nicotiana tabacum* L. of normally grown and those grown under irradiation from a Co^{60} gamma source were sectioned and compared.

2. In the material studied the stain-take of the normal tobacco stem apices was of such a nature that support for the "anneau initial" of Plantefol (1947) was apparent.

3. In irradiated stem apices periclinal divisions were observed in the first tunica, a layer which in normal plants is not observed to divide in any way but anticlinally.

4. The second tunica layer of irradiated stem apices loses its recognizability as a discrete layer.

5. The anneau initial concept is supported in irradiated tips in that the periclinal divisions induced appear in the central cells of the first tunica layer, but the cells of the first tunica continued to show anticlinally oriented division pattern within the region of the anneau initial.

6. Reasons for the suggestion of possible support for the "meristeme d'attente" of Buvat (1952, 1953) are given.

7. The possible significance of the observed periclinal divisions induced in the first tunica layer of this plant is discussed.

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BULLETIN OF THE TORREY BOTANICAL CLUB

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SYNCHYTRIUM CINNAMOMEUM

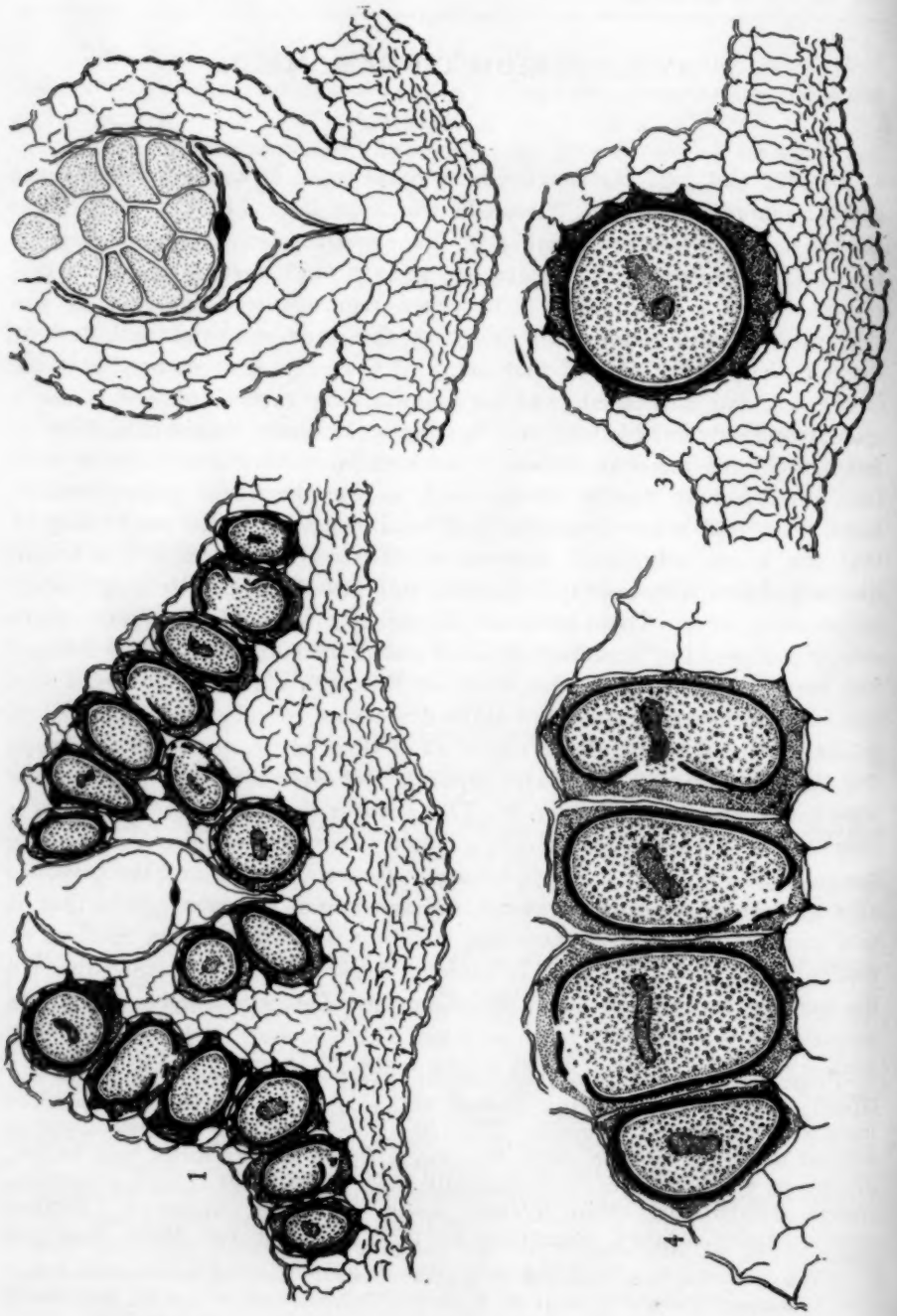
JOHN S. KARLING[1, 2]

In 1892 and 1921 Davis collected a parasite on *Ranunculus recurvatus* and *R. septentrionales* in Wisconsin which he later (1924) named *Synchytrium cinnamomeum* because of its cinnamon-brown appearance on the hosts. He reported the occurrence of only small resting spores in this species, and for this reason it has been regarded as a member of the subgenus *Pycnochytrium*. In studying the type material collected at Somers, Wisconsin, I found that many of the galls were unusually large, irregularly mound-shaped, and compound with several of their sheath cells secondarily infected by resting spores. In some cases up to fifty or more resting spores were present in such galls, and some of these were in turn enveloped by sheaths of their own so that the initial galls appeared to be compound heaps of smaller galls and spores. This led me to suspect that the heaps originated initially around sporangial galls which had discharged zoospores over their sheaths and onto the host cells immediately surrounding them. These zoospores apparently infected the outer sheath cells, stimulated the formation of small secondary galls, and then developed into resting spores. A careful study of the type material confirmed this suspicion in several cases, and stained sections revealed the presence of prosori, sori and sporangia or remnants of them in the center of the heaps (fig. 1). In addition single and separate non-compound sporangial galls were found on the leaves (fig. 2). This showed that *S. cinnamomeum* is a long-cycled species which develops prosori, sori, sporangia, and resting spores. Accordingly, it does not belong in *Pycnochytrium*, and the presence of a prosorus preceding the soral and sporangial stages suggests that it is a member of *Microsynchytrium*. Pending discovery of the method of resting spore germination, it is placed temporarily in this subgenus. On the basis of the present study the diagnosis of *S. cinnamomeum* may be amended as follows:

Prosori lying beneath sori in base of infected cell when empty and collapsed; plugs between empty prosori and sori ovoid, 10–13 × 12–16μ. Sori usually subspherical to ovoid, 132–150 × 152–170μ, with yellowish-orange content and thin hyaline walls. Sporangia up to 60 per sorus, polyhedral, 27–58μ in greatest diam., exceptionally large ones 66–86μ, with yellowish-orange content and thin hyaline walls. Zoospores unknown. Resting spores usually solitary, sometimes up to 3 in a cell, not filling host cell

[1] This study has been supported by a grant from the National Science Foundation.

[2] I am very grateful to Drs. H. C. Green, University of Wisconsin, and A. N. Steward, Oregon State College, for loan of herbarium material.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completely, spherical, 37–90μ, ovoid 38–53 × 42–70μ, or almost oblong, 35–55 × 60–86μ, with yellowish-golden content and amber-brown walls, 2.8–3.6μ thick; enveloped by a dense, compact, and homogeneous layer of residue which adheres closely to spore wall and fills remainder of host cell; germination unknown.

Compositely dihomeogallic, sometimes diheterogallic, galls separate and scattered or crowded and confluent, frequently compound and irregular, cinnamon-brown, almost hemispherical, mound-shaped or obtusely conical. Sporangial galls 216–325μ high by 324–370μ broad with base embedded in leaf and sometimes causing a bulge on the opposite side of leaf, cupulate after dehiscing; sheath 2–4 cells thick; sheath cells greatly enlarged and elongated outward from leaf surface. Composite resting-spore galls small, 124–204μ high by 172–212μ broad; sheath 1–2 cells thick, sheath cells greatly enlarged and elongate outward. Simple resting-spore galls 50–70μ high by 35–48μ broad.

Very few non-compound sporangial galls were found in the type material, and as is shown in figure 1, most of the sporangial galls are compounded with minute resting-spore galls. The one shown in this figure is not very irregular, but its sheath cells as well as some of the surrounding host cells are infected with resting spores. This suggests, as noted earlier, that zoospores were discharged from the sporangia within the disrupted sorus, and after emerging they infected the sheath cells as well as other host cells in the immediate vicinity of the sporangial gall. However, this suggestion is based entirely on appearances in stained sections of herbarium material and needs to be confirmed from study of living material. If the development of such galls occurs as suggested, their origin is somewhat similar to that of the compound galls induced by *S. succisae*. In the latter species, however, the zoospores seem to be released in the base of the initially infected cell and then infect the inner lateral and basal sheath cells, according to Schroeter's (1870) figure 10, pl. II. These enlarge, become pyriform and eventually bear 1–3 resting spores. Accordingly, the resting-spore galls and spores in *S. succisae* occur in the base of the sporangial galls. A few such galls and spores were found in the base of sporangial galls in *S. cinnamomeum* also, but most of them occur on the outside as shown in figure 1. As noted in the diagnosis, the sheath cells are usually more elongated outward than is shown in figures 1–3, but the dried herbarium material is so shrunken that it is difficult to determine the exact shape and size of these cells.

The sorus apparently develops above the prosorus because the latter was always found beneath the sorus in the base of the infected cell, as

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FIGS. 1–4. *Synchytrium cinnamomeum*. FIG. 1. Compound sporangial gall with 17 resting spores and remnants of prosorus and sorus in center. × 100. FIG. 2. Non-compound conical sporangial gall with empty prosorus beneath sorus of sporangia. × 170. FIG. 3. Composite resting-spore gall with resting spore enveloped by dense layer of residue. × 170. FIG. 4. Adjacent simple resting-spore galls. × 210.

shown in figures 1 and 2. No migration stages of the protoplasm out of the initial cell or prosorus were found, and in all cases observed the prosorus was empty and collapsed. However, that the initial cell had functioned as a prosorus was evident from the presence of a plug of densely-stainable material between the empty collapsed vesicle and sorus of sporangia. As I have shown frequently (1955a and b) such plugs are always present in species whose initial cells function as prosori, and their presence is an effective key to recognition of the occurrence of prosori even when the latter are collapsed and hardly recognizable as such. As shown in figures 1 and 2, the base of the infected cell and empty prosorus usually appear constricted after the sporangia have been formed in and released from the sorus. This apparently occurs by the expansion of the inner sheath cells around the base of the host cell. As the initial cell or prosorus discharges its content to form the sorus, psosibly the pressure is reduced, and the sheath cells expand inward causing the constriction. I (1955) found similar constrictions in *S. holwayi*, but in this species the inner lateral sheath cells had divided and were elongated at right angles to the basal portion of the infected cell.

The resting-spore galls may occur separately also on the surface of the leaf and be composite or sometimes simple. Most of them, however, are composite, but *S. cinnamomeum*, nevertheless, may be compositely dihomeogallic or diheterogallic in its effect on the host. Also, the composite resting-spore galls may be confluent or compound like the sporangial galls. As shown in figure 3, isolated non-compound composite galls usually are small with a sheath 1–2 cells thick and do not protrude conspicuously on the surface of the host. In some cases the sheath may envelope only a part of the infected cell or be reduced to a basal fringe. Thus, gradations from composite to simple resting-spore galls may be found like those caused by *S. variabilum* on *Ranunculus occidentalis*. Simple galls usually occur when numerous adjacent cells are infected, and each of these may enlarge to become a unicellular gall (fig. 4).

Usually, the resting spore does not fill the host cell completely, but the remainder of the infected cell is filled with a dense, homogeneous, reddish-brown residue which adheres closely to the spore wall. When spores are dissected out the residue usually remains attached so that the spore and residue appear almost polyhedral in surface view. In longitudinal sections (fig. 4) they appear angular like those of *S. endobioticum* in potato tissues.

In connection with *S. cinnamomeum* it may be noted that H. S. Jackson, 11–7–1914, collected an unidentified species on *Ranunculus* sp. in Oregon. A careful study of the herbarium material showed that this species is long-cycled also and develops prosori, sori, sporangia and resting spores. Al-

though germination of the resting spores has not been observed it probably belongs in the subgenus *Microsynchytrium* also. So far as can be determined from the herbarium material it has the following characteristics.

Prosori subspherical, 90–110μ, ovoid, 98–114 × 120–132μ, or almost hemispherical, 54–60 × 110–125μ, with light amber-brown walls, 1.4–2 thick; lying in base of host cell when empty. Sorus developed above prosorus, subspherical, 110–138μ, or ovoid, 92–120 × 128–136μ, with light amber-brown walls, 1.8–2.2μ thick. Plug between empty prosorus and sorus 6–10μ thick by 12–18μ diam. Sporangia 13–40 per sorus, polyhedral, 20–56μ in greatest diam. with yellow content and hyaline walls. Zoospores unknown. Resting spores usually solitary and not filling host cell completely, sometimes up to 4 in a cell, spherical, 30–60μ, ovoid, 30–66 × 54–90μ, sometimes almost polyhedral, with yellow content and smooth, amber-brown walls, 2.5–3.6μ thick; enveloping residue brown, crumbly or compact and filling remainder of cell; germination unknown.

Compositely dihomeogallic, rarely diheterogallic, galls abundant on both surfaces of leaves and on petioles, separate and scattered or crowded and confluent, sometimes compound. Sporangial galls yellow, almost hemispherical on surface of leaf, or mound-shaped, 192–240μ high by 180–312μ broad at base; sheath hyaline and 1–3 cells thick, usually turning brown after dehiscence. Composite resting-spore galls brownish, 156–180μ high by 165–190μ broad at base; sheath 1–2 cells thick. Simple galls ovoid or fusiform on petioles.

On *Ranunculus* sp., near Sulphur Springs, Ore., U.S.A. (Leg. H. S. Jackson, 11–7–1914; spec. no. 1947 in herb. Oregon State College).

It may seem surprising that sporangial galls and sporangia were so abundant in material collected as late as November in Oregon because in most long-cycled species which occur in the temperate zone such galls are reported to occur in late spring and summer. However, as more species are studied carefully throughout the seasons it will be found that the so-called summer or sporangial phase may extend into the winter months. In *S. brownii*, for instance, Mr. B. T. Lingappa, has found that prosori, sori and sporangia occur abundantly out-of-doors during December and January at Lafayette, Indiana.

Some of the large dehisced galls of *Synchytrium* sp. were cinnamon-brown like those of *S. cinnamomeum*, and contained a few sporangia which were 62–120μ in greatest diameter with dark-orange content and thick, 1.2–3.8μ, hyaline walls. These looked like sporangia which had become dormant without forming zoospores, and if this is true this is the first case of dormant sporangia to be reported in *Synchytrium*. In most of the galls, however, the sporangia were smaller and thin-walled as reported in the diagnosis above. On petioles the resting-spore galls varied from relatively small composite to simple ovoid or fusiform ones. In the latter galls the spores were usually ovoid, oblong, greatly elongate and occasionally plano-convex.

In addition to this unidentified species and *S. cinnamomeum* described above three other long-cycled species, *S. andinum, S. ranunculi* and *S. variabilum,* have been reported on species of *Ranunculus.* In all of these five species the initial cell functions as a prosorus and gives rise to a sorus above it in the upper part of the host cell. This close similarity in type of development and position of the prosorus raises the question of whether or not some of them are identical. *Synchytrium ranunculi* has smaller prosori and sori and forms fewer (4–18) sporangia per sorus than the other species, although in *Synchytrium* sp. as few as 13 sporangia may occur in a sorus. Nevertheless, *S. ranunculi* appears to be a smaller species than the other four. *Synchytrium cinnamomeum* is similar to *S. variabilum* and *Synchytrium* sp. in being occasionally diheterogallic, and its prosori, sori, and sporangia are similar to those of these species and *S. andinum.* However, *S. cinnamomeum* is the only species in which large, irregular heaped-up compound galls have been found. The content of the sori and sporangia in all species is yellowish-orange, and in addition all of them have relatively small resting spores which are enveloped by a compact layer of residue. So far germination of the spores has not been seen in any of the species, and possibly some differences may be found in this process. If not identical some of these species may prove to be very closely related, but this cannot be determined until more intensive studies are made of living material and the host range of the species is known.

SUMMARY

1. *Synchytrium cinnamomeum,* a parasite of *Ranunculus* species, which was formerly believed to be a short-cycled member of the subgenus *Pycnochytrium,* is long-cycled and develops prosori, sori, sporangia, and resting spores. Accordingly, it is transferred temporarily to the subgenus *Microsynchtrium,* pending discovery of its method of resting spore germination.

2. Another and unidentified species occurs on *Ranunculus* sp. in Oregon and resembles *S. cinnamomeum* in several respects.

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SPECIES OF CORDYCEPS PARASITIC ON ELAPHOMYCES

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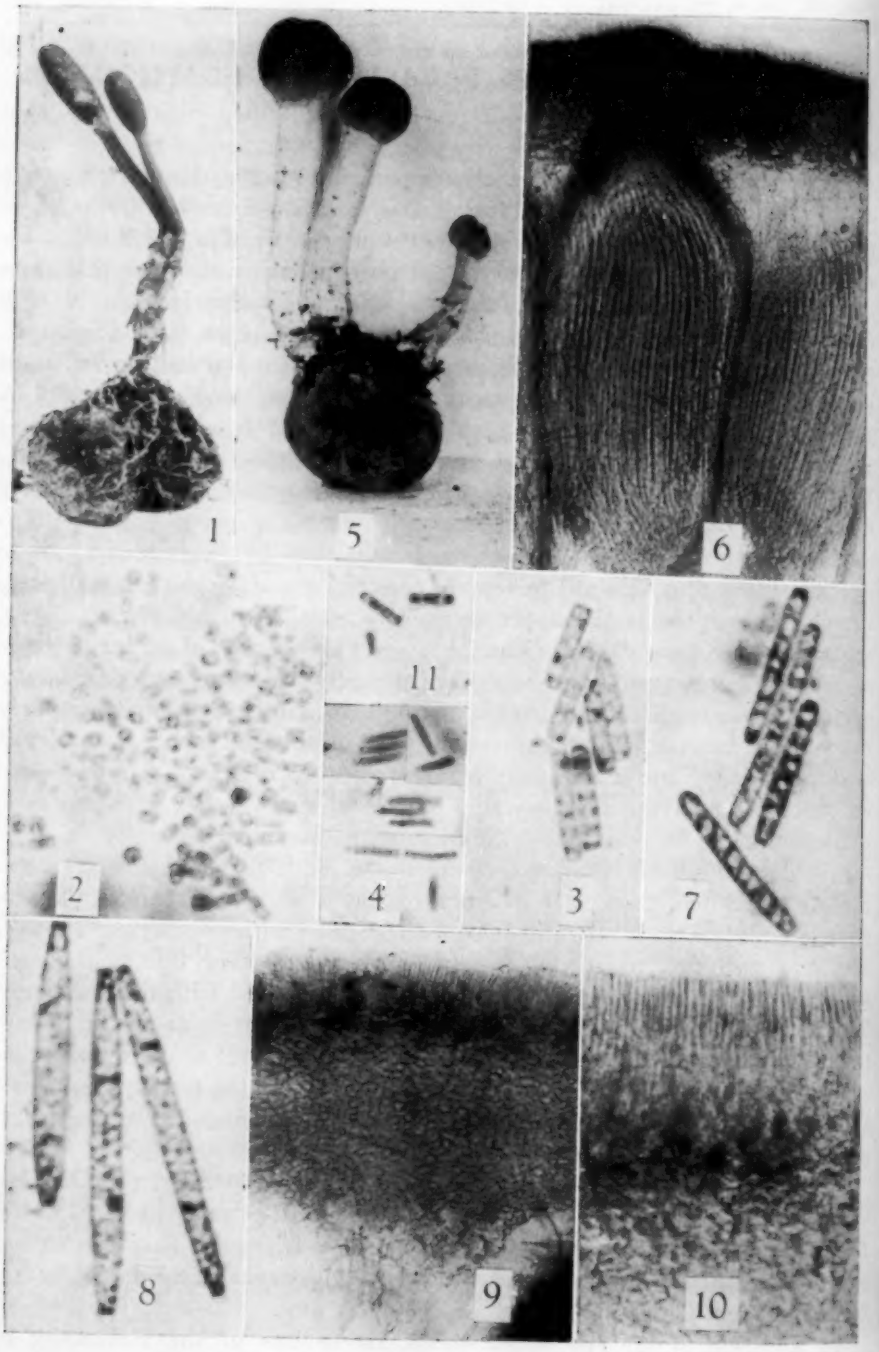
The species of *Cordyceps* which are parasitic on *Elaphomyces*, a genus of subterranean ascomycetous fungi, are very closely related. By their parasitism they are markedly separated from other species which infect insects and spiders. However in their general morphology they are similar to the other species of the genus. Two species, *C. ophioglossoides* and *C. capitata*, have been recognized on *Elaphomyces* in Europe. In addition *C. canadensis* and *C. nigriceps* have been described from North America. Both however are usually treated as synonyms of *C. capitata*. *C. intermedia*, *C. japonica* and *C. jezoensis* have been described from Japan.

The stromata of these species are elongated, either clavate or capitate. They are attached to the ascocarps of the subterranean hosts either directly as in *C. capitata* or by rhizomorphs as in *C. ophioglossoides*. The stipe consists of compact somewhat interwoven longitudinal hyphae which continue upward spreading outward to form a central core of more or less densely interwoven hyphae in the upper ascogenous portion of the stroma. Covering this upper core is the perithecial layer. This consists of an inner tissue of loosely interwoven outwardly developing hyphae and an outer dense cortex. In some species the cortex is simple, consisting of densely irregularly interwoven hyphae, pseudoparenchymatous in section. In other species it is duplex, made up of an inner layer of densely interwoven hyphae and an outer layer having short parallel hyphae at right angles to the surface, palisade-like in section. These differences are used in this study as diagnostic distinctions in the separation of species. The perithecia are completely embedded. They have well differentiated walls of a compact pseudoparenchymatous structure and short ostioles lined with periphyses. The asci are long, cylindric narrowing below. The walls are very thin, with hemispherical thickenings at the apices which are provided with narrow pores. The ascospores are hyaline, filiform, acuminate at the ends and multiseptate. They break into one-celled fragments. It is difficult to distinguish and study the ascospores and measurements are given of the part-spores. Since the terminal segments obscure differences they are excluded from the measurements which are given.

This treatment of the species for North America includes *C. ophioglossoides* and *C. capitata*. *C. nigriceps* is considered the same as *C. capitata*. *C. canadensis* is recognized as a valid species. Although *C. japonica* has not been seen from North America it probably occurs and consequently has been included. Three species are described as new.

In addition to the specimens in the Herbarium of the University of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Michigan (MICH), collections from the Farlow Herbarium (FH), the Herbarium of the New York Botanical Garden (NY), the Herbarium of the New York State Museum (NYS), the Herbarium of the University of California (UC) and the National Fungus Collections of the U.S. Bureau of Plant Industry (BPI) have been studied.[1]

KEY TO SPECIES

A. Stromata clavate, the ascogenous portion not abruptly enlarged from the stipe ..... B
A. Stromata capitate, the ascogenous portion spherical, ovoid or cylindric abruptly enlarged from the stipe ..... D
B. Cortex of the ascogenous portion having an ectal layer of short parallel hyphae palisade-like in section; segments of ascospores 6–8 × 1–1.5 μ ..... 3. *C. tenuispora*
B. Cortex of ascogenous portion without a differentiated ectal layer C
C. Ascospore-segments 2–4 × 2 μ ..... 1. *C. ophioglossoides*
C. Ascospore-segments 10–18 × 3–4 μ ..... 2. *C. japonica*
D. Cortex of the ascogenous portion having an ectal layer of short parallel hyphae palisade-like in section ..... E
D. Cortex of the ascogenous portion without a differentiated ectal layer ..... F
E. Ascospore-segments (18)24–48(54) × 4–5 μ ..... 5. *C. canadensis*
E. Ascospore-segments 3–6 × 2 μ ..... 6. *C. valliformis*
F. Ascospore-segments 8–25(32) × 2.5–3 μ ..... 4. *C. capitata*
F. Ascospore-segments 2–5 × 1.5–2 μ ..... 7. *C. fracta*

1. **Cordyceps ophioglossoides** (Fr.) Link Handbuch 3: 347. 1833. (figs. 1 & 2). *Sphaeria ophioglossoides* Fr. Syst. Myc. 2: 324. 1832. *Torrubia ophioglossoides* Tul. Sel. Fung. Carp. 3: 20. 1865. *Torrubia parasitica* Schroeter, in Cohn Krypt. Flora Schles. 3 pt. 2: 277. 1908. *Cordyceps parasitica* P. Henn. Nerthus 6: 4. 1904 according to Seaver N. Am. Flora 3 pt. 1: 53. 1910. Stromata clavate, simple or rarely branched above, 2–8 cm long, usually attached to the host by rhizomorphs; ascogenous portion one-fourth to one-half the length, not sharply enlarged from the stipe, 3–8 mm thick, reddish brown to olivaceous brown, punctate with the ostioles of the perithecia, with a cortex consisting of one layer of closely interwoven hyphae pseudoparenchymatous in section; stipes 2–8 mm thick, olivaceous to dark brown; perithecia ovoid, 600–800 × 250–500 μ, entirely embedded in the stroma; asci cylindric, narrowing below, 400–450 × 5–8 μ, with a

[1] The writer is indebted to the Curators I. Mackenzie Lamb, Donald P. Rogers, Stanley Jay Smith, Lee Bonar and John A. Stevenson for the loan of specimens for this study.

FIGS. 1–2, *Cordyceps ophioglossoides*. FIG. 1, stromata and rhizomorphs from ascocarp of Elaphomyces E.B.M. 4198 (MICH) approx. × 1. FIG. 2, part-spores, Mougeot & Nestler no. 565 × 1000. FIG. 3, *Cordyceps japonica* part-spores, type (BPI) × 1000. FIG. 4, *Cordyceps tenuispora*, part-spores, type (NY) × 1000. FIGS. 5–7, *Cordyceps capitata*. FIG. 5, stromata from ascocarp of Elaphomyces A.H.S. 17593 (MICH) approx. × 1 (photo by A. H. Smith). FIG. 6, section showing perithecia and cortex, Mougeot & Nestler no. 763, approx. × 100. FIG. 7, part-spores, Mougeot & Nestler no. 763, × 1000. FIGS. 8–10. *Cordyceps canadensis*. FIG. 8, part-spores A.H.S. 38566 (MICH) × 1000. FIG. 9, section of cortex, type (NY) approx. × 250. FIG. 10, section of ectal layer of cortex, type (NY), approx. ×375. FIG. 11, *Cordyceps fracta*, part-spores, type (MICH) × 1000.

hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled segments 2–4(5) × 1.5–2 μ.

On *Elaphomyces cervinus, E. granulatus, E. muricatus, E. variegatus* and *Elaphomyces* sp.

Specimens studied: 165 from Connecticut (BPI, FH), District of Columbia (BPI), Iowa (BPI), Maine (FH, MICH, NY), Maryland (BPI, MICH), Massachusetts (FH, NY, BPI), Michigan (MICH), New Hampshire (FH, MICH, NY, BPI, UC), New York (FH, MICH, NY, BPI, NYS), New Jersey (NY), North Carolina (FH, BPI, MICH), Ohio (MICH), Oregon (MICH), Pennsylvania (NY, MICH), Rhode Island (FH, NY), Tennessee (FH, MICH, BPI), Vermont (FH, NY, BPI), Virginia (MICH, NY, BPI), Washington (MICH), West Virginia (MICH, NY), Ontario (MICH, NY, BPI), Quebec (MICH, NY, BPI).

In addition 40 specimens from Austria, Belgium, Czechoslovakia, England, Finland, France, Germany, Hungary, Italy, Russia, Switzerland, and Japan were studied. Of the exsiccati cited by Fries in the Systema, Mougeot-Nestler no. 565 has been studied and is proposed as the lectotype.

This is the most common species. It is distinguished by the small segments of the ascospores (fig. 2) which are 2–4 × 1.5–2 μ, and the clavate stromata in which the ascogenous portion is not sharply enlarged from the stipes (fig. 1). The stromata are usually attached to the hosts by rhizomorphs (fig. 1). The cortex of the ascogenous portion of the stromata is made up of very closely interwoven brown hyphae and does not have a differentiated ectal layer.

2. **Cordyceps japonica** Lloyd. Myc. Writings 6: 913. 1920. (fig. 3). *Cordyceps umemurai Imai* Trans. Sapporo Nat. Hist. Soc. 11: 32. 1929. Stromata clavate, 2.5–7 cm long, developing directly from the host; ascogenous portion one-third to one-half of the length, 4–10 mm thick, rough from projecting ostioles, black when dry, with a cortex consisting of one layer of closely interwoven brown hyphae pseudoparenchymatous in section; stipes 2–7 mm thick, dark olivaceous brown or black; perithecia ovoid; 500–700 × 250–350 μ, entirely embedded; asci cylindric, 250–400 × 7–10 μ with a hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled cylindric segments 10–18(20) × 2.5–4 μ.

On *Elaphomyces japonica*, Mikawa, Japan, J. Umemura, June 1916, type (BPI); *Elaphomyces* sp. Feldkirch, Austria, T. Murr. Oct. 1915 (FH).

Although this species has not been found in North America it probably occurs. It was originally reported by Lloyd (1916) as *Cordyceps capitata* var. *canadensis*. He later (1920) recognized it as a distinct species and named it *C. japonica*. The type from the Lloyd Herbarium of the National Fungus Collection, U.S. Department of Agriculture has been studied. As illustrated by Lloyd (1916 fig. 860, 1920 fig. 1621) the stromata are clavate with less differentiation between the stipe and ascogenous portion than in *C. ophioglossoides*. A specimen from Austria identified as *C. ophioglossoides* in the Farlow Herbarium is very similar in stromata, cortex and part-

spores. *C. japonica* is similar to *C. ophioglossoides* in clavate stromata and cortex. However, it differs in having the stromata directly attached to the host without rhizomorphs, and in having larger part-spores (fig. 3). Imai (1929) has described a clavate species, *C. jezoensis*, from Japan which has part-spores much larger 16–50 × 3.5–4.5 μ.

3. **Cordyceps tenuispora** sp. nov. (fig. 4). Stromatibus clavatis, 7 cm longis, supra 10–15 mm crassis, castaneis; cortice duplice interne pseudoparenchymato externe valliformi; stipitibus 3–5 mm crassis, flavobrunneis; peritheciis anguste ovoideis, 750–1000 × 250–300 μ, immersis; ascis cylindricis, 430–600 × 4–6 μ; ascosporis hyalinis, filiformibus, multiseptatis, in unicellularia fragmenta secendentibus 6–8 × 1–1.5 μ.

Specimen typicum: Thornton, Pennsylvania, May 27, 1919, C. F. Murphy (NY).

Stromata up to 7 cm long, clavate; ascogenous portion obovoid, 10–15 × 8–10 mm, not abruptly enlarged from the stipe, dark chestnut-brown when dried, with a cortex having an inner layer of closely interwoven brown hyphae pseudoparenchymatous in section and an ectal layer of parallel hyaline hyphae palisade-like in section; stipes 3–5 mm thick, yellowish brown; perithecia narrowly ovoid, 750–1000 × 250–300 μ, narrowing to an acute base below, narrowing to a slender neck above, completely embedded; asci cylindric 430–600 × 4–6 μ, with a hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, breaking into 1-celled cylindric segments 6–8 × 1–1.5 μ.

Host not found, probably on *Elaphomyces* sp. Thornton, Delaware Co., Pennsylvania, May 27, 1919, C. F. Murphy type (NY); Cumberland, Maryland, W. T. Lakin, Lloyd Coll. 37226 (BPI).

This species has clavate stromata. It differs from both *C. ophioglossoides* and *C. japonica* in having a cortex with a palisade-like ectal layer. The ascospores are very slender (fig. 4) and the segments are somewhat longer than those of *C. ophioglossoides* and much shorter than those of *C. japonica*. Although the hosts were not collected there is not much doubt that they are species of *Elaphomyces*.

4. **Cordyceps capitata** (Fr.) Link. Handbuch 3: 347. 1833 (figs. 5–7). *Sphaeria capitata* Fr. Syst. Myc. 2: 324. 1832. *Cordyceps nigriceps* Peck Bul. Torrey Bot. Club 27: 21. 1900. Stromata capitate, 2–11 cm long; ascogenous portion abruptly enlarged into ovoid, spherical or subcylindric heads, 5–20 × 5–15 mm, natal-brown, olive-brown to olive-black, punctate to rough from the ostioles of the perithecia, with a cortex of closely interwoven brown hyphae pseudoparenchymatous in section; stipes 2–8 mm thick, ocher-yellow, olive-buff, olive-grey to olive-black, furfuraceous; perithecia ovoid, 650–950 × 250–420 μ, entirely embedded; asci cylindric, 350–540 × 10–12 μ, gradually narrowing below, with a hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled, cylindric or somewhat fusoid segments 8–25(32) × 2.5–3 μ.

On *Elaphomyces cervinus*, *E. granulatus* and *Eaphomyces* sp.

Specimens studied: 46 from Alabama (MICH, BPI), Florida (FH, MICH, BPI, NY), Maine (NYS), Massachusetts (FH, BPI, NY, NYS),

North Carolina (BPI), Oregon (MICH), South Carolina (BPI, NY), Virginia (MICH), Washington (MICH), Manitoba (BPI), Quebec (BPI). Exsiccati: Ravenel Fungi Car. Fasc. 5: 48.

Specimens from Belgium, France and Hungary have been studied, including exsiccati, Flora Hungarica Exsiccata Cent. 1 Fungi 8; Mougeot and Nestler Stirpes Cryp. Vog.-Rhen. 763; Rehm Ascomycetes 1186b, Roumeguère Fungi Gall. Exs. 781; Westendorp et Wallays Herb. Crypt. Belg. 21.

One of the results of this study has been the discovery that two species have generally been included in *Cordyceps capitata*. Both have capitate stromata (fig. 5). One has the segments of the ascospores cylindric or slightly fusoid (fig. 7), 8–25 × 2.5–3 μ and the cortex of the ascogenous portion of the stroma consisting of closely interwoven brown hyphae without a differentiated ectal layer (fig. 6). The other has the segments of the ascospore more or less fusoid (fig. 8), mostly 24–48 × 4–5 μ, often with the end walls thickened and has a cortex of two layers (fig. 9). The inner layer consists of closely interwoven brown hyphae (fig. 9). The outer layer is made up of short parallel hyaline or slightly brown hyphae which are at right angles to the surface of the stroma forming a palisade layer (fig. 10). *C. capitata*, has been mostly described as having the larger spore segments but specimens of both are in herbaria under that name and both occur in Europe. It is not possible to determine to which the name *Sphaeria capitata* Fr. applies from the description given by Fries in the Systema. However he gives the following citation "Moug.! Crypt. exs. C. VIII. ined." This evidently refers to Mougeot et Nestler, Stirpes Cryptogamae Vogeso-Rhenanae 763 which was issued in 1823 a year after the publication by Fries. Three specimens of this number at the New York Botanical Garden and the Farlow Herbarium have been available for study. They have cylindric part-spores (12)14–22(32) × 2.5–3 μ and a cortex of densely interwoven hyphae without a differentiated ectal layer (figs. 6 & 7). The Mougeot-Nestler no. 763 is accepted in this study as the lectotype of the species *C. capitata*.

Peck (l.c.) described a species *Cordyceps nigriceps* which he distinguished from *C. capitata* by "free margin of the club" and narrow spore segments. He describes the segments of the ascospores as cylindric 20–40 × 4 μ. The specimen of *Cordyceps nigriceps* collected by C. L. Fox in Maine labeled type in the Herbarium of the New York State Museum has been studied. It consists of one broken stroma. The segments of the ascospores are cylindric, 14–22 × 3 μ and the cortex does not have a differentiated ectal layer. The ascogenous portion projects slightly downward over the stipe. It appears to be *C. capitata* as recognized here.

5. **Cordyceps canadensis** Ell. & Everh. Bull. Torrey Bot. Club 25: 501. 1898. (figs. 8–10). *Torrubia capitata* sensu Tul. Sel. Fung. Carp. 3: 22. 1864. *Cordyceps agariciformia* Seaver in part, N. Am. Flora 3 pt. 1: 53.

1910. Stromata capitate, 5–8 cm long; ascogenous portion abruptly enlarged into spherical, ovoid or subcylindric heads, 6–17 × 5–17 mm brown, olive-brown to black, punctate or roughened from the ostioles, with a cortex of closely interwoven brown hyphae pseudoparenchymatous in section having a well differentiated ectal layer of short hyaline or brownish parallel hyphae palisade-like in section; stipes 3–8 mm thick, yellow, olive-yellow, olive-brown or black, furfuraceous; perithecia ovoid, 550–1000 × 270–450 μ, entirely embedded; asci cylindric 300–550 × 12–16 μ, gradually narrowing below, with a hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled, subfusoid segments, (18)24–48 × 4–5 μ, often with the end walls thickened.

On *Elaphomyces granulatus, E. muricatus, E. variegatus* and *Elaphomyces* sp.

Specimens studied: 58 from Alabama (MICH), Connecticut (FH), Delaware (NY), District of Columbia (BPI), Florida (NY, FH, BPI), Kentucky (NY, BPI), Maine (NY, FH), Maryland (BPI), Massachusetts (NY, FH, NYS, BPI), Michigan (MICH), New Jersey (NY), New York (MICH, CU, NY), Pennsylvania (BPI, NYS), Tennessee (FH, MICH), Virginia (BPI), Ontario (NY, FH, BPI, MICH), Mexico, Hidalgo (MICH).

Four specimens from Germany have been studied including Rehm Ascomycetes 1186; Sydow Myc. March. 279; Rabenh.-Winter-Pazschke Fungi Europ. 3957.

This species has been generally included in *Cordyceps capitata*. The species was described by Ellis and Everhart (l.c.) from a collection made by Dearness no. 2641 at London, Canada. They state that the ascospores separate "into cylindric segments, 10–20 (mostly 15) × 2–2.5 μ". It is emphasized that "the slender cylindrical segments of the sporidia are only about half as long and wide as in *C. capitata* (Holmsk.) and very different from the globose-ellipsoid joints of the sporidia of *C. ophioglossoides* (Ehr.)."

Among the specimens in the Ellis Herbarium which is now in the Herbarium of the New York Botanical Garden is a packet bearing the label "*Cordyceps canadensis* Ell. & Dearness". This is pasted over writing on the flap of the packet which viewed by transmitted light reads as follows "Scarcely more than a form of *C. ophioglossoides*. 2641. *Cordyceps canadensis* Ell. & Dearness". Below on the packet is written "When fresh quite different from *C. ophioglossoides*, stipe shorter and stouter, head capitate, joints of sporidia oblong or fusoid 15 μ, asci 300–325 × 7–8 μ. Seems to agree with capitata except that joints are 15 instead of 25–40 μ. Joints 12–15 × 2–2½. 12–20." These measurements have been crossed out and written on the packet in another handwriting is "joints 30–45 μ long". This appears to be the specimen from which *Cordyceps canadensis* was described. It consists of a stipe and a portion of a spherical head. The cortex consists of two definite layers (fig. 9), an inner of closely interwoven hyphae and an ectal layer of short palisade hyphae (fig. 10). The segments

of the ascospore are fusoid (26)36–48 × 4 μ with the end walls thickened. With the emphasis which Ellis placed upon the small size of the spore segments in distinguishing the species *C. canadensis* this is puzzling. While Ellis' description agrees with that of *C. capitata* as treated here the specimen is not that species but is the other species which has been commonly described as *C. capitata*. It seems necessary therefore to use the name *C. canadensis* for it. This species has the largest part-spores of the species which have been found in North America (fig. 8). Imai (1929) has described a species *C. jazoensis* from Japan with part-spores 16–50 × 3.5–4.5 μ. This has clavate stromata similar to *C. ophioglossoides*.

6. **Cordyceps valliformis** sp. nov. Stromatibus capitatis, 5–7 cm longis; capitulis spheroideis vel ovoideis, 3–15 × 3–12 mm, atrobrunneis; cortice duplice interne pseudoparenchymato externe valliformi; stipitibus 1–5 mm crassis, atrobrunneis; peritheciis ovoideis, 500–700 × 200–350 μ, immersis; ascis cylindricis, 230–460 × 6–8 μ; ascosporis hyalinis, filiformibus, multiseptatis, in unicellularia fragmenta secendentibus 3–8 × 2 μ.

Specimen typicum: Highlands N. Carolina, Aug. 1933, V. K. Charles (BPI).

Stromata capitate, 5–7 cm long; heads spherical or ovoid, 3–15 × 3–12 mm, abruptly enlarged from the stipe, dark brown with a cortex having an inner layer of closely interwoven brown hyphae pseudoparenchymatous in section and an ectal layer of short hyaline parallel hyphae palisade-like in section; stipes 1–5 mm thick, dark brown, smooth or furfuraceous; perithecia ovoid, 500–700 × 200–350 μ, entirely embedded; asci cylindric, 230–460 × 6–8 μ, with a hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled cylindric segments 3–8 × 2 μ.

On *Elaphomyces cervinus* and *Elaphomyces* sp. Highlands N. Carolina Aug. 1933, V. K. Charles, type (BPI); Virginia Oct. 10, 1938, Dr. Jones FP 86265 (BPI); Mountain Lake, Giles Co. Virginia, Sept. 2–4, 1936, D. H. Linder (FH); Potterville, Ulster Co. New York, Aug. 8, 1922, H. D. House (NYS); Petawana Forest, Ontario, Sept. 1, 1947, A. H. Smith 26425 (MICH).

This species differs from *C. canadensis* in having much smaller segments of the ascospores. From *C. capitata* it differs in having a differentiated ectal layer of the cortex and smaller segments of the ascospores. *C. intermedia* Imai (1934) in Japan is similar in size of segments of the ascospores. It is described as attached to the host by short rhizomorphs. Information is not available concerning the cortex. Collections which Kobayasi (1941) has reported from Japan as *C. capitata* may belong here. He describes and figures a differentiated palisade-like ectal layer for the cortex. He however gives the segments of the ascospores as more fusoid and 13–23 × 2–4.5 μ.

7. **Cordyceps fracta** sp. nov. Stromatibus capitatis, 1.5–2.5 cm longis; capitulis sphaeroideis, 2.5 mm crassis, purpureoatris; cortice pseudoparenchymato; stipitibus 0.5–1.0 mm crassis, flavoviridis vel olivaceis; peritheciis ovoideis, 500–600 × 250–350 μ, immersis; ascis cylindricis, 300–480 ×

5–6 μ; ascosporis hyalinis, filiformibus, multiseptatis, in unicellularia fragmenta secendentibus 2–5 × 1.5–2 μ.

Specimen typicum: Cades Cove, Great Smoky Mts. Nat. Park, Tenn. Aug. 18, 1938, A. H. Smith 10334 (MICH).

Stromata capitate, 1.5–2.5 cm long, arising directly from the host; heads 2.5 mm in diameter, purplish black, with a cortex of closely interwoven brown hyphae pseudoparenchymatous in section without a differentiated ectal layer; stipes slender, 0.5–1.0 mm thick, yellowish green to olivaceous; perithecia ovoid, 500–600 × 250–350 μ, entirely embedded; asci cylindric, 300–480 × 5–6 μ, with wall hemispherically thickened at the apices; ascospores hyaline, filiform, multiseptate, breaking into 1-celled cylindric segments 2–5 × 1.5–2 μ.

On *Elaphomyces appalachensis*. Known only from the type specimen.

The specimen upon which this species is based was previously reported as *C. intermedia* Imai (Mains 1939). According to the description given by Imai, *C. intermedia* has larger stromata attached to the host by rhizomorphs and somewhat larger, specially wider, segments of the ascospores. *C. fracta* has part-spores (fig. 11) similar to *C. valliformis* which differs in having a differentiated ectal layer to the cortex.

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A STUDY OF BOTRYOPTERIS GLOBOSA DARRAH[1]

WILLIAM H. MURDY AND HENRY N. ANDREWS, JR.

As a result of several recent investigations the genus *Botryopteris* has become one of the better known assemblages of fossil plants assigned to the coenopterid ferns. Studies of the vegetative parts have been contributed by Delevoryas and Morgan (1954), Long (1943), Mamay and Andrews (1950), and Surange (1952), and the spore-bearing organs have been treated by Darrah (1939) and Mamay (1950).

Several interesting problems remain unsolved and, as a result of certain unique variations in the morphology and anatomy, a certain degree of controversy exists in the interpretation of the shoot system of several species in the genus. It is indeed problematical as to just where the distinction lies between stem and leaf, or whether it is possible to apply these terms in the same way that they are used in the modern higher plants. There is evidence to indicate that in some species the frond developed a distinct lamina while in others it did not. The massive sporangiate organs are unparalleled in the plant kingdom and although no doubt exists as to the general correlation of these with the vegetative remains we have no clear understanding as to just how the fertile parts were borne on the plant.

Darrah's original description of *Botryopteris globosa* was based on several specimens from Iowa coal-balls. These consisted of massive aggregations of thousands of sporangia, borne in terminal clusters on the ultimate ramifications of the frond or specialized fertile portions of the frond. It is our purpose to elucidate certain aspects of these fossils, as follows:

1. In addition to having several of the original specimens available for study we have obtained others from Illinois and Kansas. These were studied first to determine whether or not more than one species was present in the American material; when it was evident that they were all referable to one they were used to supplement our study of the Iowa material. This does not imply that all botryopterid sporangia from the American coal fields belong to one species but only that the characteristic massive fructifications found to date seem to be.

2. A study has been made of the highly complex frond or branch system that composes the framework of the fructification and, although we have avoided any comprehensive taxonomic considerations, some attention is devoted to the matter of correlating *B. globosa* with vegetative specimens reported by other authors.

3. Of particular interest is the striking morphological distinction between the peripheral sporangia and those lying deeper within the fructifica-

[1] A study aided by a grant from the National Science Foundation.

tion. This was not mentioned in Darrah's report although it was considered in some detail by Renault (1875) in his study of what is apparently a closely related species from France.

Material. In his original account of *B. globosa* Darrah cited eight specimens from the Shuler and Urbandale coal mines of Dallas County, Iowa, on which his description was based; two of these (#42159 and #42635) were designated as cotypes. Through the courtesy of Dr. Elso Barghoorn four specimens were placed at our disposal which were accompanied by a label bearing the number 42160[2] (one of the eight numbers assigned to the species in the original collections cited by Darrah, 1939, p. 158). There is some question as to whether these four fragments represent a single fructification since it was not possible to assemble them in a way that left no doubt in the matter. Nevertheless it is clear that all four represent the same species and they have yielded very significant information. Numerous peel preparations have been made from these four blocks which have been designated #42160-A, B, C and D.

We have also had available for study a specimen (#CB1004[3]) from West Mineral, Kansas, collected by Dr. S. H. Mamay and another (#CB856[3]) from Berryville, Illinois, the latter specimen being a particularly well preserved one.

It was imperative to determine at the outset whether or not the Iowa, Illinois and Kansas specimens represented distinct species. All compared closely in their massive size and general organization and a detailed comparison of the sporangia and spores revealed no significant differences. Since it has been shown that spore shape and sculpturing may vary markedly in different species of *Botryopteris* (Mamay 1950, as demonstrated for *B. fecunda*, *B. spinosa* and *B. illinoensis*) this seems to confirm beyond a doubt that our specimens all represent one species.

General organization. *Botryopteris globosa* is, as the specific name implies, a nearly globose structure attaining dimensions of $5 \times 5 \times 6$ cm. according to Darrah. The additional specimens that we have from Illinois and Kansas are of approximately the same size and form. So far as we are aware no other group of plants presents such a massive unit sporangial aggregate. It may be noted that we have under study in our laboratory another, presumably coenopterid, fern represented by a somewhat comparable aggregation of sporangia and we have been informed by Dr. S. H. Mamay that he has recently completed a study of another sporangial aggregate which is assigned to a new coenopterid genus. While it is not implied that this is a character common to all coenopterids there is now the suggestion that several were so constituted.

[2] This and the two previous numbers refer to the Paleobotanical collections of the Botanical Museum, Harvard University.

[3] Paleobotanical collections, Washington University, St. Louis.

The fructification consists of an apparent frond unit which displays, in the larger branch orders, the characteristic w-shaped trace of *Botryopteris*. This branch system divides profusely, the ultimate terminations bearing clusters of several sporangia, each attached by a short stalk. The sporangia, except at the periphery, are closely appressed and we have calculated, on the basis of a spherical fructification 5 cm. in diameter that the number of sporangia would be approximately 50,000.

Branching pattern within the fructification. One of the more complete Iowa specimens at our disposal contained a rather large *central strand* which we believe connected the fructification with the rest of the plant. We still do not know how the fructification was attached and it is therefore not possible to correlate this strand with portions of the frond such as the latter is known, for example, in *B. trisecta*. This species is mentioned since one of our fertile specimens is from the Berryville, Illinois locality from which *B. trisecta* was derived and Delevoryas and Morgan have more recently described specimens from the same place which may represent the more terminal portions of the frond of *B. trisecta*. It may be noted that in the latter species the authors (Mamay and Andrews 1950, text fig. 4) suggested that the sporangia were borne on the branches of that part of the frond referred to as the "proximal pinna trace". The evidence from *B. globosa* indicates that the sporangia were not borne in such a position. We will, therefore, simply refer to this major branch in the fructification as a *central strand*.

The central strand is elliptical (fig. 19) the large and small diameters measuring 7.5 and 4.5 mm. respectively while the contained vascular strand measures 2. × 0.7 mm. This central strand was followed for a distance of 12 mm. using serial peel preparations. A reconstruction of the branching pattern that develops through this distance is shown in figure 1 and certain detailed aspects of it are illustrated in figures 10 to 17.

Through the distance of 12 mm. five secondary traces (fig. 1, s.t.) were observed to depart, in a distichous arrangement, approximately every 2 mm. Figures 10 to 13 illustrate phases in the development of a secondary trace; in figure 10 an outer arm of the central strand trace (toward lower part of photo) is somewhat extended and becomes conspicuously more so in figures 11 and 12, while in figure 13 the secondary trace (indicated by heavy black line) is separate and is beginning to pass out through the cortex of the central strand. It is evident, therefore, from this series of photos that the secondary strand trace originates from a lateral arm of the central strand trace and that the latter immediately regains its "internodal" form after the departure of the secondary trace which then assumes a less clearly defined tridentate shape.

The secondary traces branch before leaving the central strand cortex, the peripheral limits of which are represented by the dotted line in figure 1.

Next, figures 14 through 17 show a series of phases in the development of the tertiary trace. In figure 14 part of the trace of the central strand is shown in the upper part of the photo while the secondary trace appears in the lower center. The surrounding clear area presumably represents decayed phloem and inner cortex. In figure 15 a conspicuous bulge is evident in the secondary trace which is nearly free in figure 16 and distinctly so in figure 17 (indicated by the heavy black line at lower right); this tertiary trace is designated as t.t. in figure 1. The secondary trace may run nearly parallel to the central strand trace for a short distance, producing another tertiary, or it passes out of the cortex without any further branching.

After their departure from the cortex of the central strand all branches undergo accelerated division. The mode of this branching is probably identical with the foregoing but the diminutive size of the traces prevents confirmation of this. Following any one of the secondary strands, then, leads to a profuse pendant branch system extending out about 2 cm. and down a distance of 1 cm. Figure 4 shows a penultimate branch near the periphery of the fructification with portions of three terminal branchlets and figure 18 shows the termination of one of the latter with several sporangia attached.

Sporangial structure and organization. *Botryopteris globosa* is of particular interest by virtue of the overall massive organization of the fructification and because of the distinctive morphology of the sporangia borne at the periphery. As a matter of orientation it will perhaps be helpful to briefly describe the sporangial sequence going from the periphery toward the interior of the fructification before entering upon a detailed description.

The fructification is ringed by a peripheral zone of sporangia which are frequently somewhat distorted in shape, usually empty of spores, and display relatively large cells. The peripheral position of these sporangia is shown at the left in figure 4 and their unique structure is shown in figures 5 and 6. The typical structure of the sporangia lying within this peripheral zone is shown in figure 8; it will be noted that the cells composing the wall (annulus cells for the most part) of these sporangia, which make up the great bulk of the fructification, are conspicuously smaller than the corresponding cells of the peripheral sporangia. Between these two types are other sporangia (fig. 7) which are more or less intermediate in form.

It may be noted at this point that Renault in 1875 reported a rather similar apparent dimorphism in his description of *Botryopteris forensis;* this was repeated in his monumental treatise on the fossil flora of Autun and Épinac (Renault 1893–1896). He described a fragment of the sporangial mass or "inflorescence" of *B. forensis* as measuring $5 \times 3 \times 3$ to 4 cm. and referred to the specialized peripheral sporangia as "sterile", noting that they were smaller than the interior (fertile) ones and concluded that they served a protective function. We wish to suggest an explanation other

than that of specialization for protection but it is in order at this point to consider in some detail the sporangia composing *B. globosa*.

The internal or "fertile" sporangia. The structure of the sporangia was determined from serial peel preparations and from several sporangia that were isolated by maceration of small portions of one of the petrifactions in dilute hydrochloric acid. The latter technique involved treatment of a thin slice of the fossil material in the acid for several days. Most of the liberated

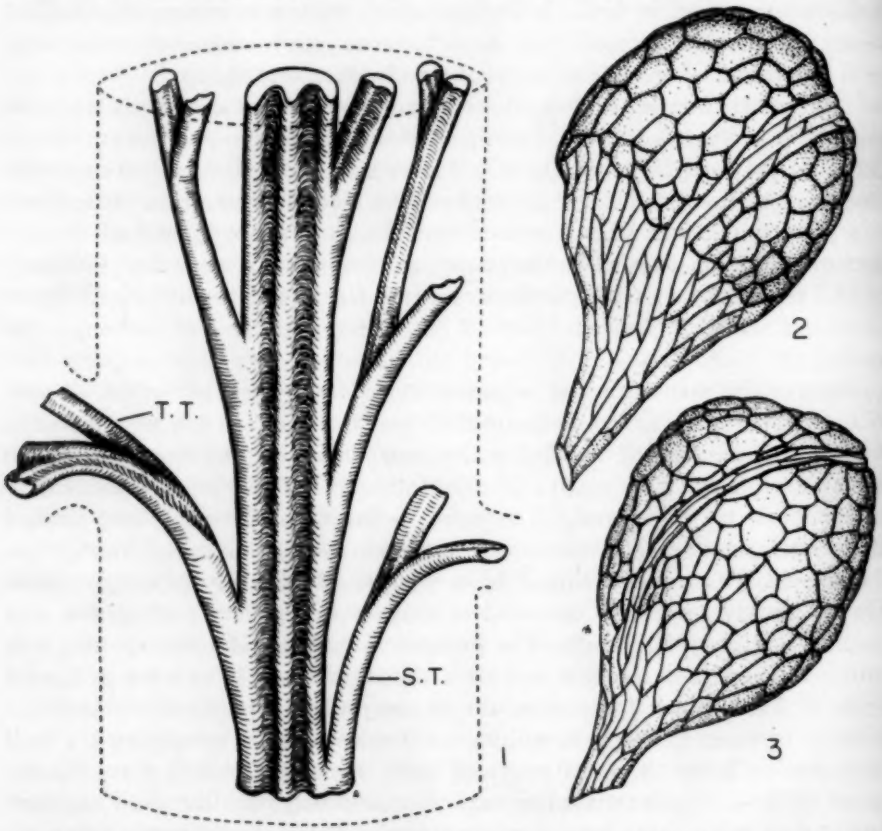
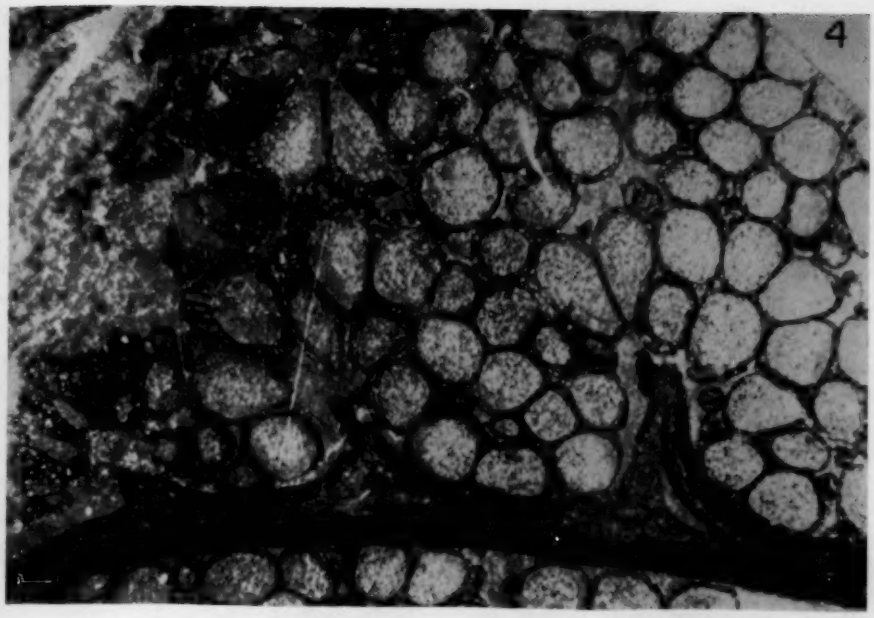


FIG. 1. A portion of the vascular system of the central strand of the fructification with five secondary traces (S.T.) departing and several tertiary traces (T.T.). The dotted line represents the outer limit of the cortex. FIGS. 2 and 3. Opposite sides of a sporangium, drawn from a specimen isolated by maceration.

sporangia were fragmentary but a few were obtained that were complete or nearly so. Figures 2 and 3 were drawn from an essentially complete sporangium isolated in this fashion. In sectional view the sporangia appear as those shown in figures 8 and 18.

Each sporangium is attached to a terminal branchlet by a very short stalk (fig. 18). For the most part the sporangia are somewhat distorted due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to dense crowding (fig. 4) but their shape in median longitudinal section (fig. 8) is essentially pyriform and nearly circular in a transverse section; they average 1.4 mm. in length and 1.0 mm. in diameter.

The sporangia possessed a double layered wall although the inner one was evidently fragile and is not regularly preserved. This inner layer of cells (fig. 9) consisted of periclinally elongated cells with oblique end walls; the cells measure up to 10 μ long and 2 μ wide. Remnants of this layer were observed in numerous sporangia including the peripheral ones (figs. 6, 7).

The sporangia obtained by maceration were particularly helpful in interpreting the general organization of the conspicuous outer layer of cells. Referring to figures 2 and 3 it may be noted that there are three cell types or regions composing this outer layer of cells: *first*, on one side of the sporangium about one third of the proximal area consists of rather thin-walled, elongate cells (fig. 2); the distribution of these cells is excentric and does not occupy as great an area on the opposite side (fig. 3); *second*, the greater part of the sporangium wall is composed of cells that are somewhat thicker walled and appreciably larger, particularly in their radial dimension, thus lending a raised appearance at the line of junction with the thin walled cells described above, although this character is more pronounced on one side than the other; these cells will be referred to as the annulus; *third*, a narrow band of elongate, prismatic cells which run longitudinally around the sporangium, thus segregating the massive annulus into two more or less equal areas; these cells functioned as the line of dehiscence.

As noted above the spores in all of the specimens at our disposal are essentially identical. They are spherical in shape (figs. 20, 21) with a trilete commisure and although quite uniform in size we have observed them to range from 40 to 55 μ in diameter; they possess a wortose to obervermiculate sculpturing of the exine.

The peripheral and intermediate sporangia. The internal or "fertile" sporangia described above are surrounded by a peripheral zone of sporangia that are strikingly distinct. The two zones intergrade through intermediate forms but it is a sufficiently rapid transition as to lend a very distinctive appearance to this peripheral region of the fructification. It is tentatively assumed that we are dealing with a centripetally directed maturation process and the following description has been drafted accordingly. We shall consider first the peripheral sporangia in their fully mature form.

In all of the specimens that we have studied the peripheral zone is present although its thickness varies somewhat. For the most part it is 2 to 3 sporangia deep but in certain areas as many as 10 to 12 are present;

FIG. 4. A portion of the peripheral part of the fructification showing three ultimate branchlets. No. 42160-B7; 12×. FIG. 5. Several of the peripheral sporangia, one of which still contains some spores. No. 42160-B9; 44×.

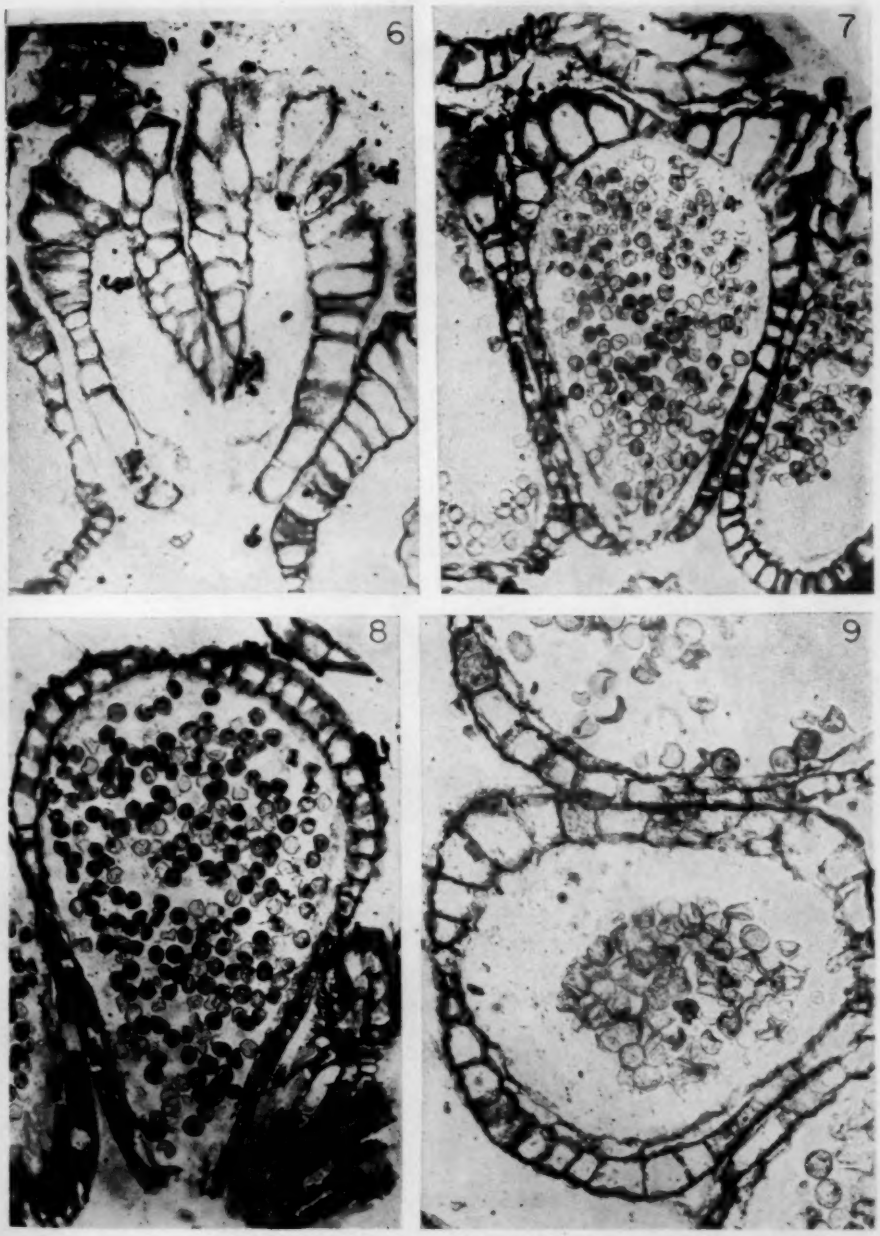
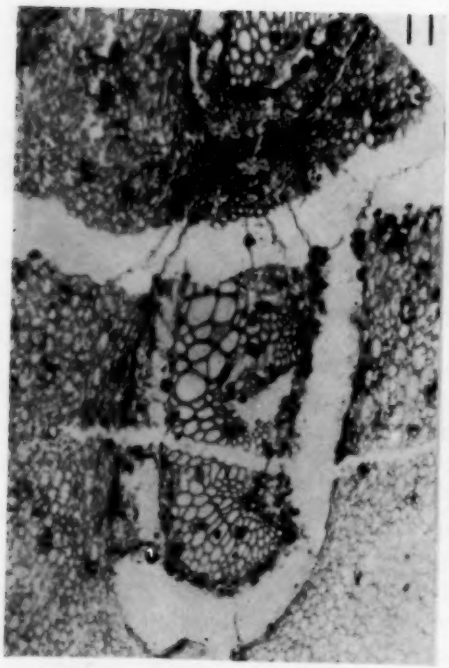


FIG. 6. A peripheral sporangium which has apparently discharged its spores. FIG. 7. A near-peripheral sporangium. FIG. 8. A sporangium from deeper within the fructification. FIG. 9. Sporangia showing the inner layer of wall cells. All from No. 42160; 50×.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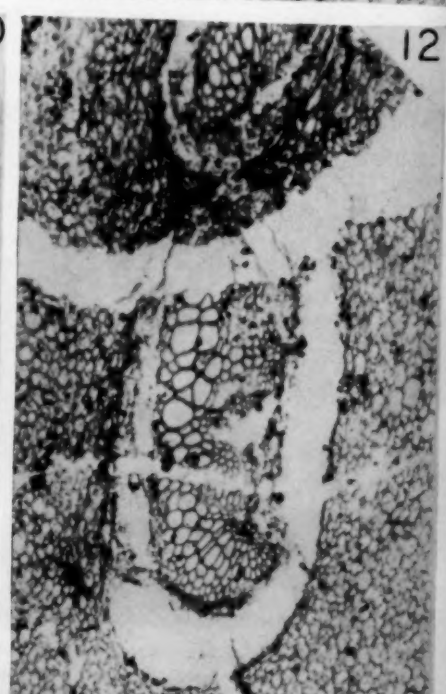
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the irregular arrangement of the sporangia prevents citation of an exact number. The sporangia are characterized by annulus cells, particularly toward the distal end of the sporangium, which are greatly elongated in a radial direction and which contain conspicuous brownish to black contents. It is noteworthy that these contents are most pronounced in the sporangia at the extreme periphery.

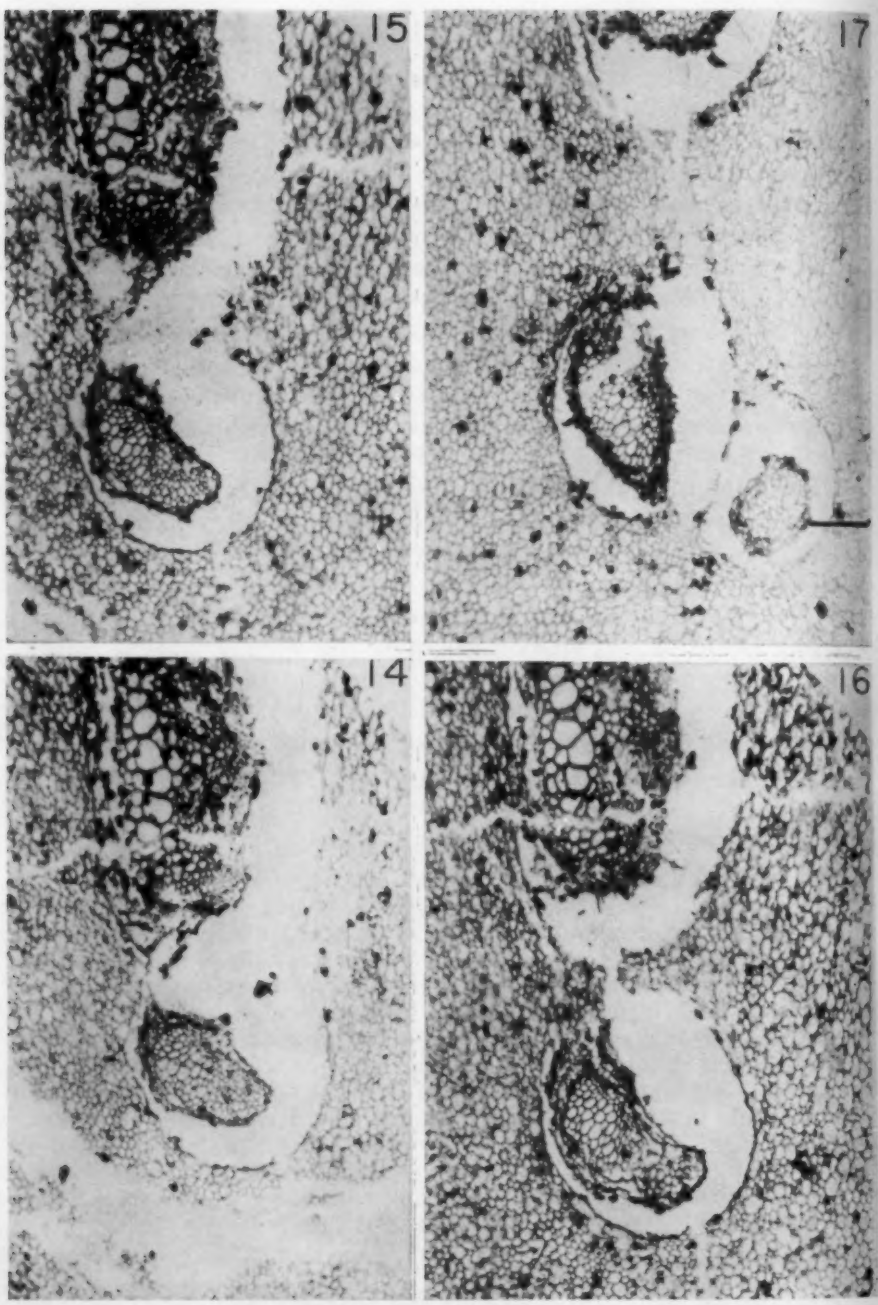
Most of these peripheral sporangia are empty of spores, often somewhat distorted and broken in a way that suggests normal dehiscence; in this feature they seem to compare with modern ferns in which the sporangia dehisce rather vigorously, expand and reflex several times, and finally remain open, or close in irregular ways. For example, we interpret the sporangium illustrated in figure 6 as one that has dehisced and partially turned in upon itself as a final stage of dehiscence.

Upon careful examination a considerable number of sporangia may be observed between the internal and peripheral zones which are intermediate in the degree to which the annulus cells are developed. Although an almost endless number of examples could be illustrated to show this transition, figure 7 is representative. The annulus cells here are about midway in size between those of typical interior sporangia (fig. 8) and those of fully developed peripheral ones (fig. 6). Most of these intermediate specimens retain their spores which suggests that dehiscence took place in a late stage of development. The conspicuous sporangium in the upper center of figure 5, with strongly developed distal annulus cells, typifies the structure of the peripheral members yet it may be noted that it contains a few spores, presumably some that were not discharged.

Botryopteris globosa Darrah, emend. Murdy and Andrews. A massive, globose aggregation of sporangia measuring approximately $5 \times 5 \times 6$ cm.; attached to the plant on which it was borne by a botryopterid frond fragment measuring 7.5 by 4.5 mm. which contains a w-shaped trace; the latter gives off two rows of appendages which divide profusely bearing several sporangia on each ultimate extremity; entire fructification consists of upwards of 50,000 closely crowded sporangia; sporangia are pyriform measuring about 1.5 mm. long and 1.0 mm. in diameter with a massive annulus occupying about three fourths of the area of the sporangium; the annulus is divided into two more or less equal parts by a longitudinal band of 2–3 rows of elongate thin-walled cells; sporangia around the periphery of the fructification characterized by greatly enlarged, radially elongate cells in the distal region; spores spherical, trilete, with a wortose to obervermiculate sculpturing and range in size from 40–55 μ.

This amended description is based on the following specimens: No. 42160, four fragments. Paleobotanical collections, Botanical Museum, Har-

FIGS. 10–13. Four stages in the departure of a secondary trace (lower part of each photo) from the central strand. The secondary trace (indicated by black line, is free in figure 13. FIG. 10. No. 42160-D78. FIG. 11. No. 42160-D85. FIG. 12. No. 42160-D91. FIG. 13. No. 42160-D97. All 28×.



FIGS. 14–17. Four stages in the division of a secondary trace showing the departure of a tertiary; the latter, indicated by a black line, is free in figure 17. FIG. 14. No. 42160-D29. FIG. 15. No. 42160-D35. FIG. 16. No. 42160-D41. FIG. 17. No. 42160-D56. All 28×.

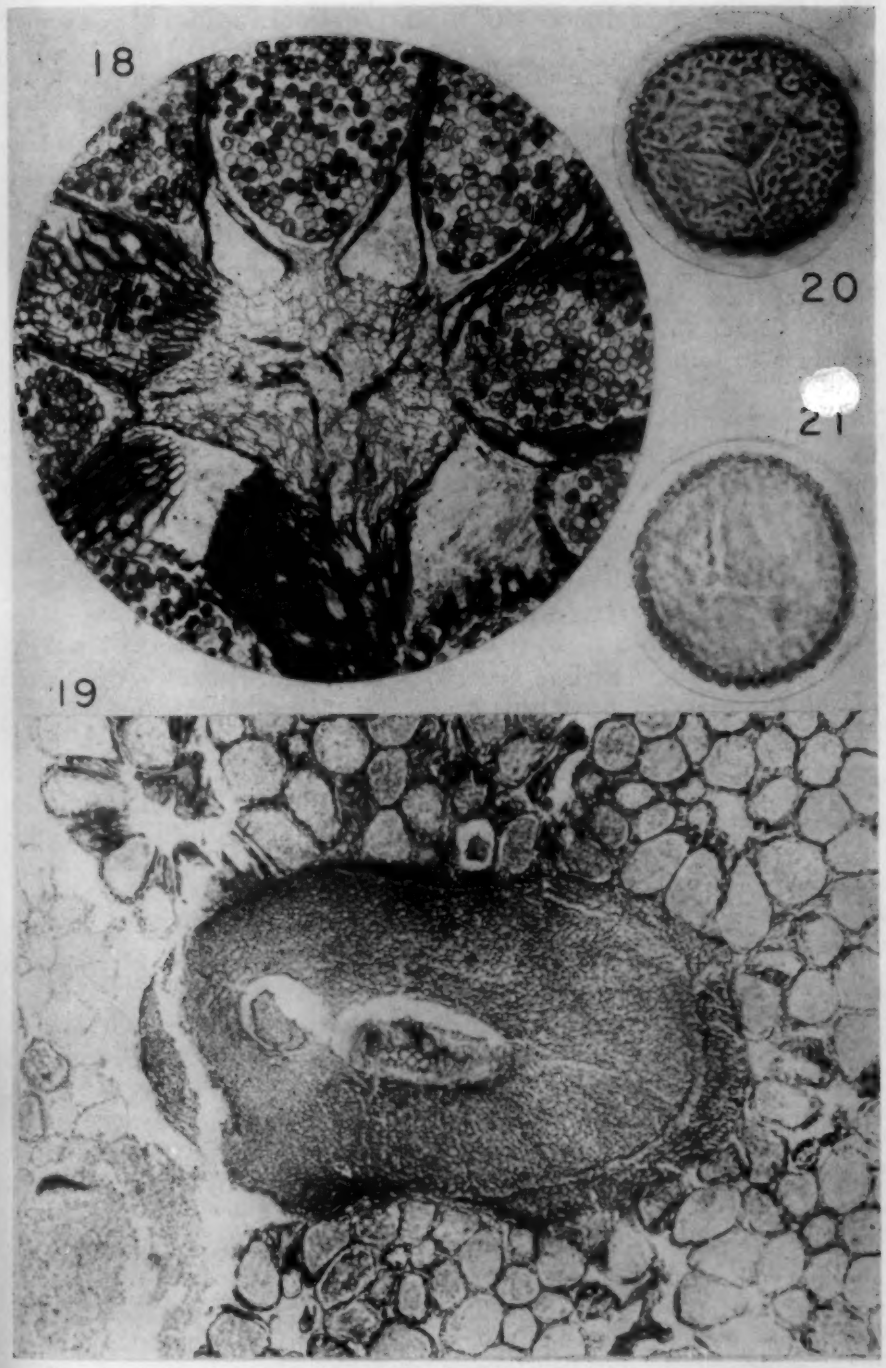


FIG. 18. A terminal branchlet of the fructification showing several sporangia attached. No. 856-A-t49; 35×. FIG. 19. The central strand showing a secondary branch departing. No. 42160-D39; 11×. FIGS. 20, 21. Spores from specimen No. 856; about 760×.

vard University. Shuler coal mine, Dallas County Iowa; Coal No. 7, Des Moines group, Pennsylvanian. No. CB856. Paleobotanical collections, Washington University, St. Louis. Brian farm, Berryville, Illinois; Calhoun coal ball horizon, McLeansboro group, Pennsylvanian. No. CB1004. Paleobotanical collections, Washington University, St. Louis. Strip mine of Pittsburgh & Midway Coal Co., approximately 4 miles south of West Mineral, Kansas; Fleming coal, Cherokee shale, Des Moines group, Pennsylvanian.

Discussion. Several intriguing and unique problems are presented by *B. globosa* and since there is no other plant with which it can be compared at all closely, other than Renault's *B. forensis*, our only recourse seems to be to consider these on their own merits.

Aside from its massive size the most problematical feature of the fructification is the distinctive zone of peripheral sporangia. We wish to consider three possible explanations although no one of them seems to effectively eliminate all doubts.

1. Renault referred to the specialized peripheral members as "sterile" sporangia on the assumption that they did not produce spores and served a protective function. This explanation is reasonable and is not to be readily discredited although it does not seem to be a wholly satisfactory answer at least as far as our American material is concerned. Renault's rather well executed illustrations leave little doubt that the two species functioned in essentially the same fashion but since it has not been possible to study his preparations our conclusions are based on the material at hand.

The first question that arises is the nature of the protective function that the peripheral sporangia presumably served; it may be suggested that they functioned as an indusial structure to prevent dessication of the interior sporangia in the early stages of development.

If our assumption is correct that the sporangia matured progressively toward the center of the fructification it is likely that this function was served at least inadvertently.

2. A second explanation which deserves some consideration is that we are dealing with a maturation process. This view is supported by the fact that the peripheral sporangia appear to have dehisced in a normal fashion, a few still retain some of their spores (fig. 5), and sporangia are frequently encountered which are intermediate, in the development of the annulus cells (fig. 7), between the typical peripheral ones (fig. 6) and those within (fig. 8).

Evidence which militates against this view lies in the fact that the annulus cells of the interior sporangia (fig. 8) appear to be mature and several botanists who have examined our preparations have objected to the likelihood that these could have undergone further development.

3. A third explanation is that the fructification was dimorphic, pro-

ducing sporangia of a different type at the periphery which may have served a protective function or in some other capacity that is not known.

It is difficult to avoid the assumption that there was some correlation between the diversity of sporangial morphology and the spore dispersal mechanism of the fructification. In order that dispersal should have been accomplished by all, or at least a significant number of the sporangia, it would seem that the branch system of the fructification must have expanded as a whole, or that the peripheral sporangia fell away progressively after spore discharge or that a combination of these two phenomena played a part in the dissemination of the spores.

Taking the several factors into consideration that have been noted above we tentatively postulate that the apparent dimorphic sporangial morphology is the result of a maturation process. The most significant evidence in support of this is the fact that there is actually a continuous sequence in sporangial morphology between the interior ones and those at the extreme periphery. Toward the outside of the central region sporangia are encountered with slightly larger annulus cells, ones that are markedly so (fig. 7), and others with fully mature annuli (fig. 5) which may contain all of their spores, only a few or none at all.

It cannot be denied that this was a rather unique maturation process in that it must have taken place rapidly in the final stages of sporangial development and one that was confined to the annulus cells since the spores throughout the fructification all exhibit the same degree of maturity.

In answer to the objection that the annular cells of the interior sporangia were too mature to have been able to undergo this pronounced development it may be noted that the annular cells are not extremely thick-walled at any time. In the case of living plants instances are known in which cells undergo reversible wall development; for example, the thick-walled endosperm cells of the date palm, persimmon and others become thinner at germination and collenchyma cells are known to become thinner-walled when the phellogen originates in this tissue (see Esau, 1953, pp. 175, 188).

It is, therefore, our concept that in the general development of the fructification the spores matured completely and probably uniformly throughout. This was followed by a final maturation process of the annulus cells which progressed in a centripetal direction, the outermost sporangia maturing first and as these fell away the ones immediately within developed to maturity and in turn discharged their spores.

As previously stated there is, so far as we are aware, no homologue among living ferns which compares at all closely with the organization or presumed developmental mechanism of *B. globosa*. It may be noted, however, that in *Gleichenia pectinata* sori, consisting of 10 to 12 tightly clustered sporangia, are occasionally encountered in which some of the sporan-

gia are undehisced because of the pressure exerted by juxtaposed sporangia (Bower 1923, p. 210). This has suggested to us the possibility that dehiscence may not have taken place at all in the great bulk of the interior sporangia of *B. globosa* and that it did indeed evolve a potentially productive but actually highly inefficient reproductive organ which may in part account for the extinction of the group.

Affinities of B. globosa. There are several reasons why it is not opportune to attempt a correlation of the fertile material described here with *Botryopteris* species that are known only from vegetative specimens. It is evident from recent studies (particularly Delevoryas and Morgan 1954, Mamay and Andrews 1950, Surange 1952) that we are only beginning to acquire a clear understanding of the general morphology of this interesting group of plants.

One of the specimens on which the present account is based (No. CB856) was obtained from the same locality (Berryville, Illinois) from which *B. trisecta* (Mamay and Andrews 1950) as well as the specimens described by Delevoryas and Morgan (1954) were derived. In the case of *B. trisecta* it seems evident that only the basal portions of the fronds were preserved and although it was suggested that one of the basal pinna branches, in which a terete vascular strand is found, may have been fertile this seems to be disproven by the presence of the distinct w-shaped strands found in our *B. globosa* material. Very little information was obtained from the specimens described as *B. trisecta* concerning the central petiolar trace and the distal part of the frond but Delevoryas and Morgan have noted that the specimens they worked with may constitute this missing part of *B. trisecta*. We have recently obtained a large coal-ball specimen from Berryville containing a much greater abundance of the shoot system of this species than has been available previously. Although it will require some time to study it in detail it is hoped that when we have done so the facts we have to date may be fitted into a more unified picture.

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Acknowledgements. We wish to acknowledge the generous cooperation of Dr. Elso S. Barghoorn in placing specimens at our disposal from the original collections of this interesting fossil; thanks are also due Dr. Sergius H. Mamay for the Kansas specimen and Ellen K. Lissant for assistance with the drawings composing figures 1–3.

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TWO SMALL SPECIES OF CONIDIOBOLUS FORMING LATERAL ZYGOSPORES

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The two readily culturable entomophthoraceous fungi herein described as new species of *Conidiobolus* came to light in Petri plates of maizemeal agar that had been canopied with small quantities of leaf mold gathered under deciduous trees in northern Wisconsin and in eastern Mississippi. To hold the finely fragmented detritus securely aloft it was affixed to circular pieces of sparingly moistened filter paper, about 55 mm. wide, which were then made to adhere centrally to the ceilings of the Petri dishes. The pieces of filter paper, between 20 and 25 square centimeters in area, were found capable of holding securely a quantity of detritus weighing 30 to 50 milligrams when air-dry. On each ceiling a peripheral zone, 15 to 20 mm. wide, was left unoccupied as a provision against early contamination of the agar plate with molds that commonly grow out from the decaying material, first spreading horizontally to the rim of the glass lid and then pushing downward along the inner surface of the vertical wall.

As the Wisconsin detritus had been stored indoors for 20 months following its collection, and the Mississippi detritus had been gathered after several weeks of dry summer weather, both samples of decaying material had been exposed to prolonged desiccation. Evidently the hyphal segments and asexual reproductive bodies of all species of *Conidiobolus* had perished, for no early development of any fungus referable to this genus was observable in the canopied cultures. Despite their having somewhat greater endurance than conidia or vegetative cells, the hirsute resting spores of *Delacroixia coronata* (Cost.) Sacc. & Syd. emend. Gallaud (1905) must also have succumbed, since this ubiquitous species, which through its rapid mycelial growth and strong conidial propulsion often overwhelms the less obtrusive forms, failed to develop altogether. To encourage the after-ripening and germination of any *Conidiobolus* zygospores that might be present in the adhering detritus the filter-paper canopies were kept suitably moist and at intervals of 7 days were removed to a bed of firm absorbent cotton and there irrigated with distilled water. After such irrigation each freshened canopy was affixed to the lid of a newly sterilized Petri dish and thus superposed over a new maizemeal-agar plate. No entomophthoraceous fungi appeared during the first two weeks but during the third and fourth weeks several species of *Conidiobolus* were obtained. Among them were the 2 new forms presented herein, both of which came from detritus that had remained

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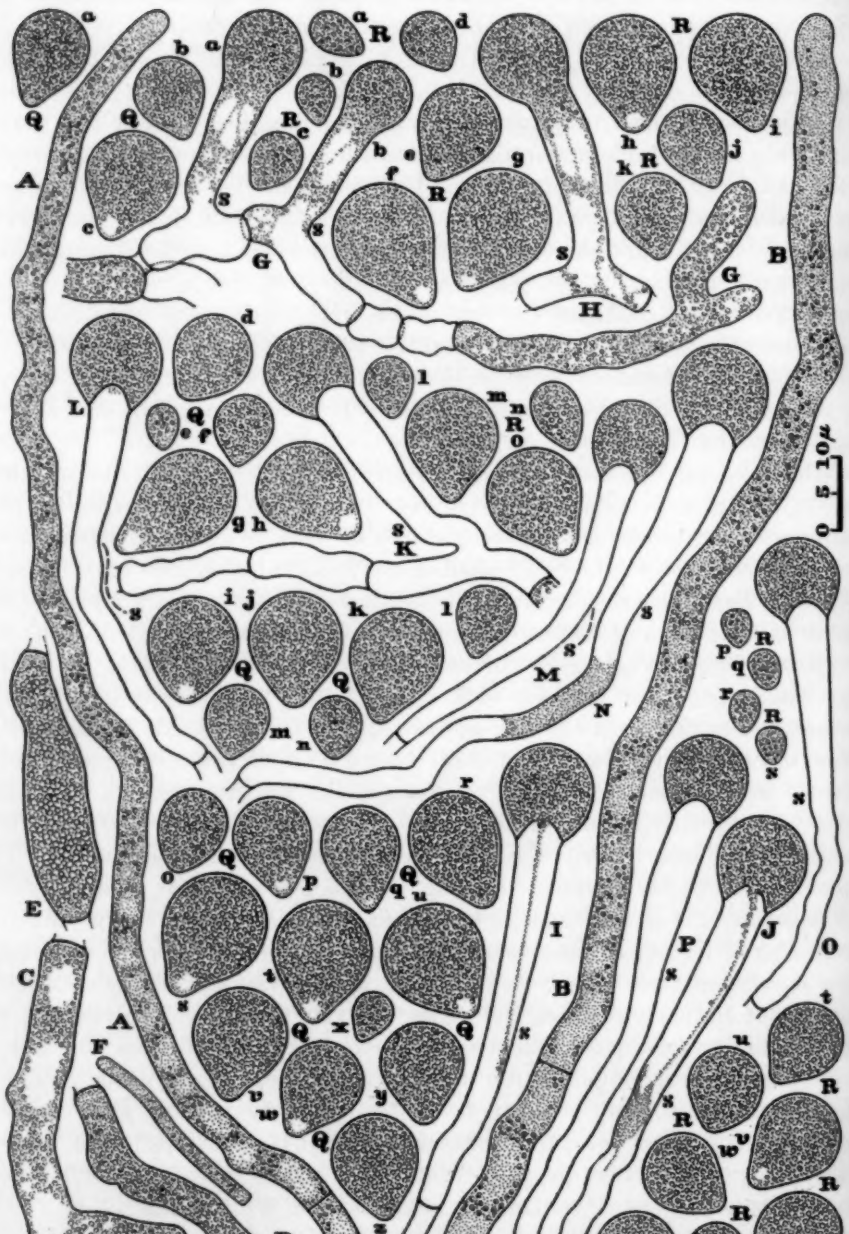
affixed to moist filter paper more than 20 days, and had thus been twice irrigated and twice placed anew over fresh agar substratum.

As various readily culturable Entomophthoraceae can be isolated from small quantities of plant detritus taken at random, whether in Wisconsin or in Mississippi, these fungi would seem distributed very widely and very thoroughly in vegetable materials that have undergone slow and somewhat prolonged decay in moist contact with the ground. In view of their extensive distribution and ubiquitous occurrence there can be little doubt that these fungi exist much more abundantly in nature than has long been supposed. Except perhaps in localities where very numerous insects, such as house flies, grasshoppers, aphides and seventeen-year cicadas, are being, or recently have been, parasitized on a massive scale, the species of *Conidiobolus*, *Delacroixia* and *Basidiobolus* must persist collectively in far greater quantity than the insectivorous species assigned to the genera *Empusa*, *Entomophthora* and *Massospora*.

While among the insectivorous Entomophthoraceae host relationships are very helpful in establishing correct distinctions between species, no characteristic relations to the components of various plant detritus have been observed that might be of similar use in defining species of *Conidiobolus* and *Basidiobolus*. The host relationships set forth in descriptions of species of *Empusa* and *Entomophthora* are often durably attested in dried parasitized insects kept as herbarium specimens; and from many of these parasitized specimens, besides, rather satisfactory microscope mounts of asexual and sexual reproductive apparatus can be prepared. In contrast, owing to extensive collapse and disappearance of membranous parts and to very pronounced disintegrative changes in cellular contents, mounts prepared from dried cultures of species of *Conidiobolus* and *Basidiobolus* usually reveal only poorly the morphology shown in living material. It appears unlikely, for instance, that the difference in sculpture of zygospore wall whereby the 2 new species of *Conidiobolus* are most conspicuously distinguished will in distant years be clearly recognizable in the relevant dried specimens that have been deposited in the National Fungus Collections, Plant Industry Station, Beltsville, Maryland. To make up partly for the shortcomings of the dried specimens the accompanying figures (fig. 1–4) show at a uniform magnification assortments of reproductive bodies that are intended on a small scale to be imitative of the random assortments displayed in microscope mounts prepared from living material. For needs of the less remote future pure cultures of the new species have been supplied to the American Type Culture Collection in Washington, D. C.

1. **Conidiobolus paulus** Drechsler sp. nov. Mycelium incoloratum, vulgo aliquid inconspicuum; hyphae steriles mediocriter ramosae, saepe paulo pravae, plerumque 1.5–7 μ (vulgo 4–5 μ) crassae, mox septatae, postea hic illic disjunctae vel inanitae, in cellulis 20–300 μ longis constantes; fertiles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hyphae simplices, incoloratae, in aerem 15–30 μ ad lucem protendentes, itaque in parte protendenti erectae vel acclives, ibi sursum latescentes, apice 3.5–7 μ crassae; conidia violenter absilientia, incolorata, globosa vel obovoidea, basi papilla 1–5 μ alta et 2–7 μ lata praedita, in totum 5–19 μ longa, 4–14 μ lata; zygosporae evidenter saepe ex conjunctione cellularum duarum hypharum genitae, a latere prope commissuram oriundae, plerumque sufflavae, quandoque ellipsoideae sed saepissime globosae, vulgo 10–15 μ crassae, muro semper levi 0.8–1.8 μ crasso circumdatae.

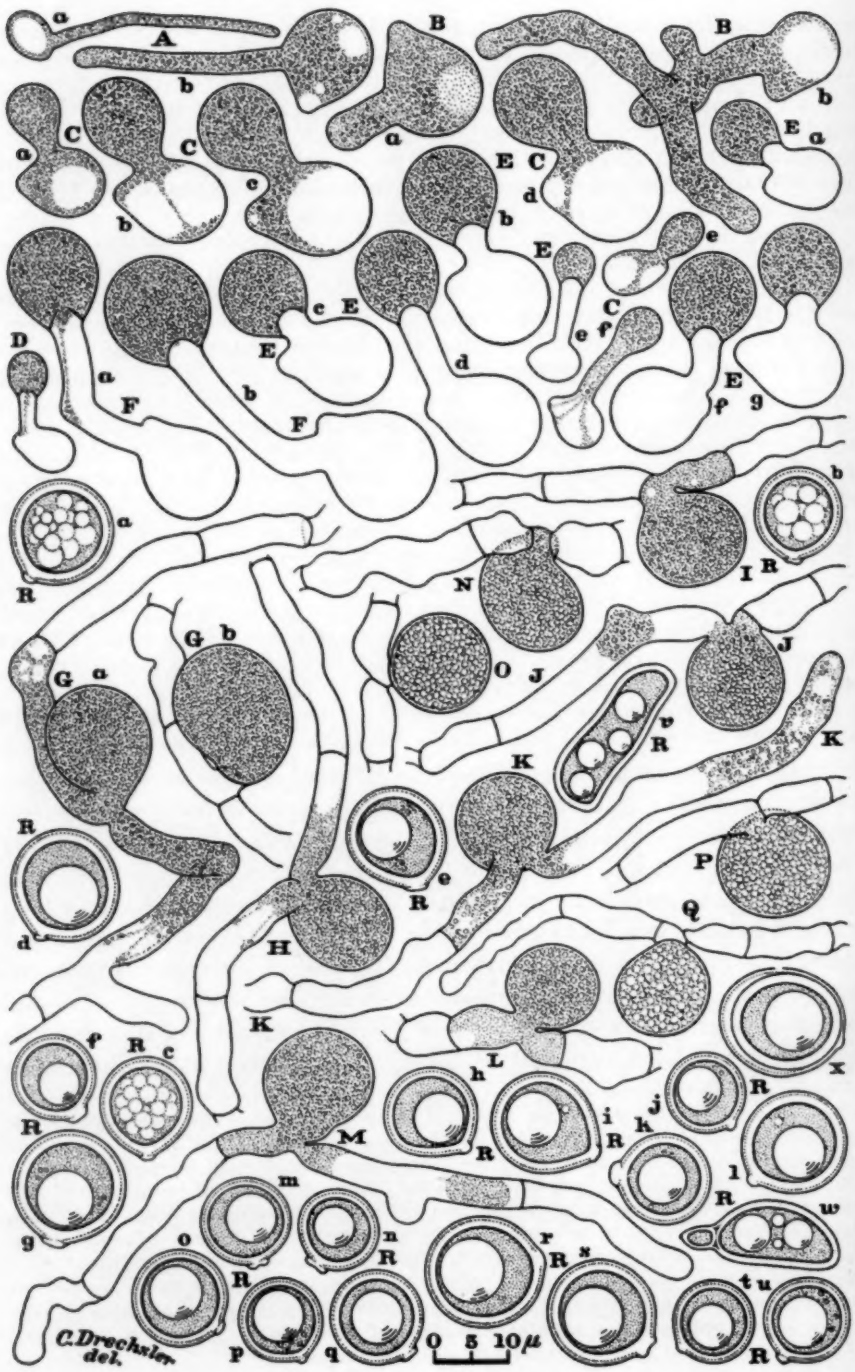
Habitat in foliis arborum (*Aceris, Betulae, Ulmi*) putrescentibus prope Park Falls, Wisconsin.

Mycelium colorless, usually rather inconspicuous; assimilative hyphae moderately branched, sometimes rather markedly crooked, 1.5 to 7 μ (commonly 4 to 5 μ) wide, soon becoming partitioned by cross-walls, when actively growing commonly terminating in a segment 100 to 300 μ long, the other segments being often 20 to 100 μ long and in many places becoming disjointed from one another or separated by empty portions of tubular membrane; conidiophores colorless, unbranched, extending 15 to 30 μ into the air toward the main source of light, the aerial portion (whether erect or inclined) widening upward to an apical diameter of 3.5 to 7 μ; conidia springing off forcibly, colorless, globose or obovoid, 4 to 14 μ wide, 5 to 19 μ in length inclusive of a basal papilla mostly 1 to 5 μ high and 2 to 7 μ wide; zygospores commonly formed laterally near apical union of two segments supplied by separate hyphal branches, usually distinctly yellowish when mature, sometimes ellipsoidal but more often subspherical, mostly 10 to 15 μ in diameter, always smooth except for a slight hilar protuberance, surrounded by a wall 0.8 to 1.8 μ thick.

Isolated from decaying leaves collected in deciduous woods (mainly of maple, birch and elm) near Park Falls, Wisconsin, on November 18, 1954.

Because of the small dimensions of its mycelial hyphae as well as of its reproductive parts *Conidiobolus paulus* belongs in a category with the two dwarfish congeneric species I described earlier (Drechsler 1955a, 1955b) under the binomials *C. pumilus* and *C. nanodes*. When its mycelium grows actively on agar containing some finely ground maizemeal in suspension the relatively long terminal segments (fig. 1, A, B) at the advancing margin commonly vary from 4 to 5 μ in width. The shorter segments, which, one after another, are delimited from the proximal end of the terminal segments, may later become widened to 6 or 7 μ, and, in addition, may undergo modification in shape through extension of branches and protuberances

FIG. 1. *Conidiobolus paulus* as found in maizemeal-agar cultures; ×1000. A, B, Distal portions of two main hyphae at margin of a mycelium. C, D, Hyphal segments about 1 mm. from mycelial margin. E, Somewhat indurated hyphal segment in culture 15 days old. F, Small hyphal segment in culture 15 days old. G, Procumbent hyphal branch with two young conidiophores, a and b; s, surface of substratum. H, Young conidiophore arising from a procumbent hyphal segment; s, surface of substratum. I, J, Distal portions of two nearly mature conidiophores arising from submerged hyphal segments; s, surface of substratum. K, Mature conidiophore arising from procumbent hypha; s, surface of substratum. L-P, Distal portions of five mature conidiophores arising from submerged hyphal segments; s, surface of substratum. Q (a-z), R (a-z), Detached conidia showing usual variations in size and shape.


C. Drechsler del.
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(fig. 1, C, D). In maizemeal agar cultures 15 days old, segments as much as 8 or 9 μ in width (fig. 1, E) are sometimes found isolated in scattered positions, their strongly granulose contents and noticeably thickened walls being expressive, however, more of a resting than of a vegetative condition. Aging cultures show likewise much less massive segments, including some only 1.5 to 2 μ wide (fig. 1, F), that migrate slowly through the agar in pushing forward at the tip while constantly withdrawing protoplasmic materials from the rear portion. These migrant segments originate as germ hyphae extended by small conidia (fig. 2, A, a) into substratum already thoroughly occupied by mycelium of the fungus.

Asexual reproduction takes place freely in maizemeal-agar cultures of *Conidiobolus paulus*. The phototropic conidiophores extended directly into the air from procumbent hyphal segments (fig. 1, G, a, b; H; K), as also the phototropic aerial prolongations (fig. 1, I, L-P) of narrow hyphae extended from submerged segments, are comparatively short, much as in *C. pumilus* and *C. nanodes*. In gradually widening upward from the surface of the substratum (fig. 1, G-P: s) they resemble more especially the conidiophores of *C. pumilus*.

The young conidium first appears as a globose swelling on the expanded distal end of the conidiophore (fig. 1, G, a, b; H). It increases steadily in size as protoplasmic materials move into it from below. During the later stages in the upward movement of cellular contents it becomes progressively delimited at the base by an intruding partition (fig. 1, I, J). When the supporting shaft has been emptied of granular substance the central aperture of the partition is rapidly walled over. As the dome-shaped septum thus formed, besides being of only moderate convexity, is of large diameter in relation to the globose body it delimits, its everted contour in conidia that have sprung off (fig. 1, Q-R: a-z) is often found virtually in alignment with the adjacent portion of globose membrane. Consequently in *C. paulus* the papilla is not usually seen as an abruptly protruding part, but rather often forms the narrower end of a somewhat obovoid conidium.

Conidia of *Conidiobolus paulus* that spring off on to agar substratum already occupied by the fungus may germinate by extending a rather nar-

FIG. 2. *Conidiobolus paulus* as found in maizemeal-agar cultures; ×1000. A, Detached conidia, a and b, germinating on substratum already occupied by the fungus. B, Detached conidia, a and b, germinating on unoccupied substratum. C, Six conidia, a-f, each with a broad outgrowth on which a secondary conidium is being formed. D, Conidium with aerial outgrowth bearing a partly delimited secondary conidium. E, Seven conidia, a-g, each with a broad outgrowth bearing a completely delimited secondary conidium. F, Two conidia, a and b, which have each put forth a germ hypha that terminates as a conidiophore. G, Two stages of a sexual reproductive unit showing: a, zygospore in active growth; b, zygospore newly delimited 1¼ hours later. H-M, Six sexual reproductive units, each with zygospore in later stages of growth. N-Q, Four sexual reproductive units, each with zygospore newly delimited. R (a-x), Zygospores showing variations in size and shape.

row germ hypha (fig. 2, A, a, b), which in many instances will then elongate without putting forth any branches. On fresh unoccupied substratum a conidium more usually pushes out a wide germ hypha (fig. 2, B, a) that will promptly ramify (fig. 2, B, b) and grow into a mycelium. On either occupied or unoccupied substratum detached conidia display repetitional development abundantly: the individual spore extends upward a broad outgrowth that swells distally into a globose body (fig. 2, C, a-f) which on receiving all the protoplasmic contents (fig. 2, D) is delimited completely by a convex basal partition (fig. 2, E, a-g) and soon springs off as a secondary globose conidium. Sometimes, too, a broad germ hypha, which, in the beginning grew out horizontally, changes its course abruptly and thereupon elongates as a phototropic conidiophore to bear similarly a secondary self-propelling globose conidium (fig. 1, F, a, b). Owing to persistent repetitional development (fig. 2, C, a-f; D; E, a-g) cultures 10 to 20 days old show intermixed with larger conidia of recent primary origin some unusually small conidia (fig. 1, Q, e; R, p-s) among which specimens only 5 μ long or only 4 μ wide can be found. These small conidia are only slightly larger than the minute asexual spores characteristic of the entomophthoraceous tardigrade parasite *Ballocephala sphaerospora* Drechsler (1951). They are not held properly designable as microconidia since multiplicative reproduction has so far never been observed in *C. paulus*.

At temperatures near 25° C. zygospores are formed abundantly in maizemeal-agar cultures of *Conidiobolus paulus*. The earliest stages of sexual reproduction are not readily detected, as incipient zygospores look little different from the casual thickenings found here and there on mycelial filaments. Because of the haphazard crookedness of many hyphae it is not easy to infer from the angular relations of the gametangia whether a young zygospore originated through conjugation of 2 adjacent hyphal segments or through apical union of 2 branches given off from separate filaments. Nor can this be easily determined from the mycelial connections of the gametangia, for here, as in many congeneric species, emptied portions of hyphal membrane soon vanish completely. However, since the junction between the 2 gametangia (fig. 2, G, a; H-N) commonly appears as a rather pronounced constriction—an appearance not often presented when adjacent segments are concerned—it may be presumed that conjugation usually takes place between the tips of separate branches.

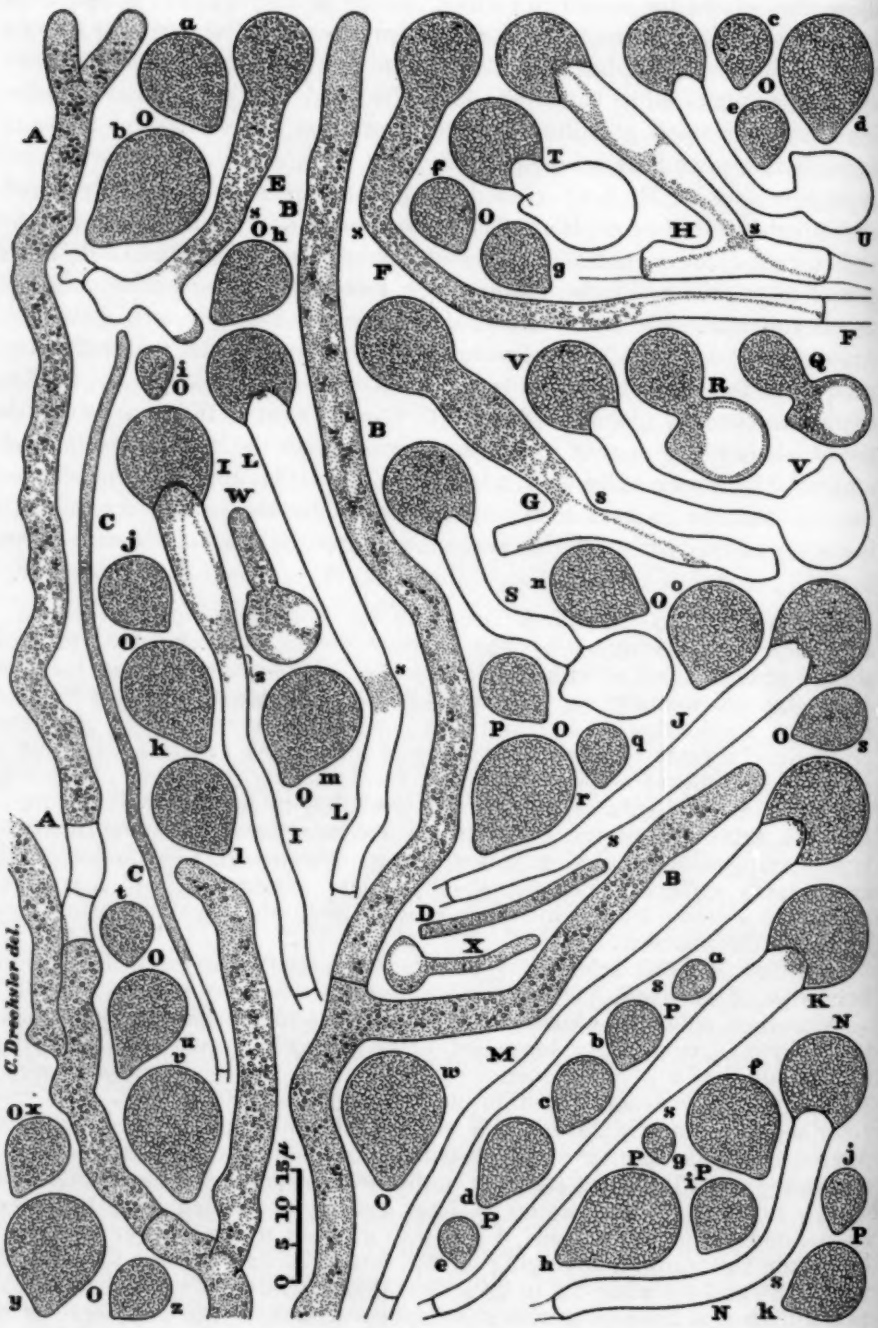
The young zygospore, in any case, buds forth laterally from one of the gametangia, arising as a globose swelling very close to the junction between the fused segments. As the gametangia become progressively emptied of protoplasm, retaining walls are laid down at intervals to mark successive stages of evacuation. When the gametangium not bearing the zygospore has been emptied of protoplasmic materials a retaining wall is usually laid

down that closes the aperture formed earlier in conjugation. A half-hour later this wall is commonly to be seen approximately 1 μ from the septum that in the meantime has been formed to delimit basally the full-grown zygospore (fig. 2, G, b; O-Q), which now is filled with protoplasm containing numerous small globules. Through continued coalescence the globules increase in size and diminish in number (fig. 2, R, a-c) until in the mature zygospore (fig. 2, R, d-u) a single large homogeneous globule is found enveloped in clear protoplasm. The yellow coloration characteristic of the ripe sexual spore would seem to reside mainly in the thickish wall layer deposited within a colorless outer layer corresponding apparently to the membrane that alone surrounded the zygospore when it was delimited. Among large numbers of zygospores a few may usually be found that depart from the normal globose type in having an elongated shape and in containing several globules (fig. 2, R, v, w). Occasionally a specimen is found which along part of its circumference shows the 2 layers of its wall separated by a space (fig. 2, R, x). In such specimens the outer layer is no less smooth than in normal zygospores, never displaying any irregularity in its round contour except in the small, somewhat variable basal protrusion.

2. **Conidiobolus undulatus** Drechsler sp. nov. Mycelium incoloratum, aliquando inconspicuum; hyphae steriles mediocriter ramosae, saepius aliquid pravae, 1.5–7 μ (vulgo 4–6 μ) crassae, mox septatae, postea hic illic disjunctae vel inanitae, in cellulis 25–250 μ consistentes; fertiles hyphae simplices, incoloratae, in aerem 15–40 μ ad lucem protendentes, in parte protendenti erectae vel acclivis, ibi sursum latescentes, subter apicem 4–8 μ crassae; conidia violenter absilientia, incolorata, globosa vel obovoidea, basi papilla 1–5 μ alta et 2.5–8 μ lata praedita, in totum 5.5–19 μ longa, 4.5–14 μ lata; zygosporae interdum ex conjunctione cellularum duarum hypharum genitae, vulgo a latere prope commissuram oriundae, raro intercalares, sufflavae, globosae vel ellipsoideae, plerumque 8–17 μ crassae, muro .7–2 μ crasso in levi interiore corio et undulato exteriore corio vulgo constante circumdatae.

Habitat in foliis arborum (praecipue *Quercus*) putrescentibus prope Starkville, Mississippi.

Mycelium colorless, sometimes inconspicuous to the naked eye; assimilative hyphae moderately branched, often somewhat crooked, 1.5 to 7 μ (commonly 4 to 6 μ) wide, soon becoming partitioned by cross-walls, when growing actively usually terminating in a segment 100 to 250 μ long, the other segments mostly 25 to 100 μ long and in many places becoming disjointed from one another or separated by short portions of empty tubular membrane; conidiophores colorless, unbranched, projecting 15 to 40 μ into the air toward the main source of light, the aerial portion (whether erect or inclined) widening upward, 4 to 8 μ in greatest width near or somewhat below the tip; conidia springing off forcibly, colorless, globose or obovoid, mostly 4.5 to 14 μ wide, 5.5 to 19 μ in length inclusive of a basal papilla 1 to 5 μ high and 2.5 to 8 μ wide; zygospores usually borne in lateral or in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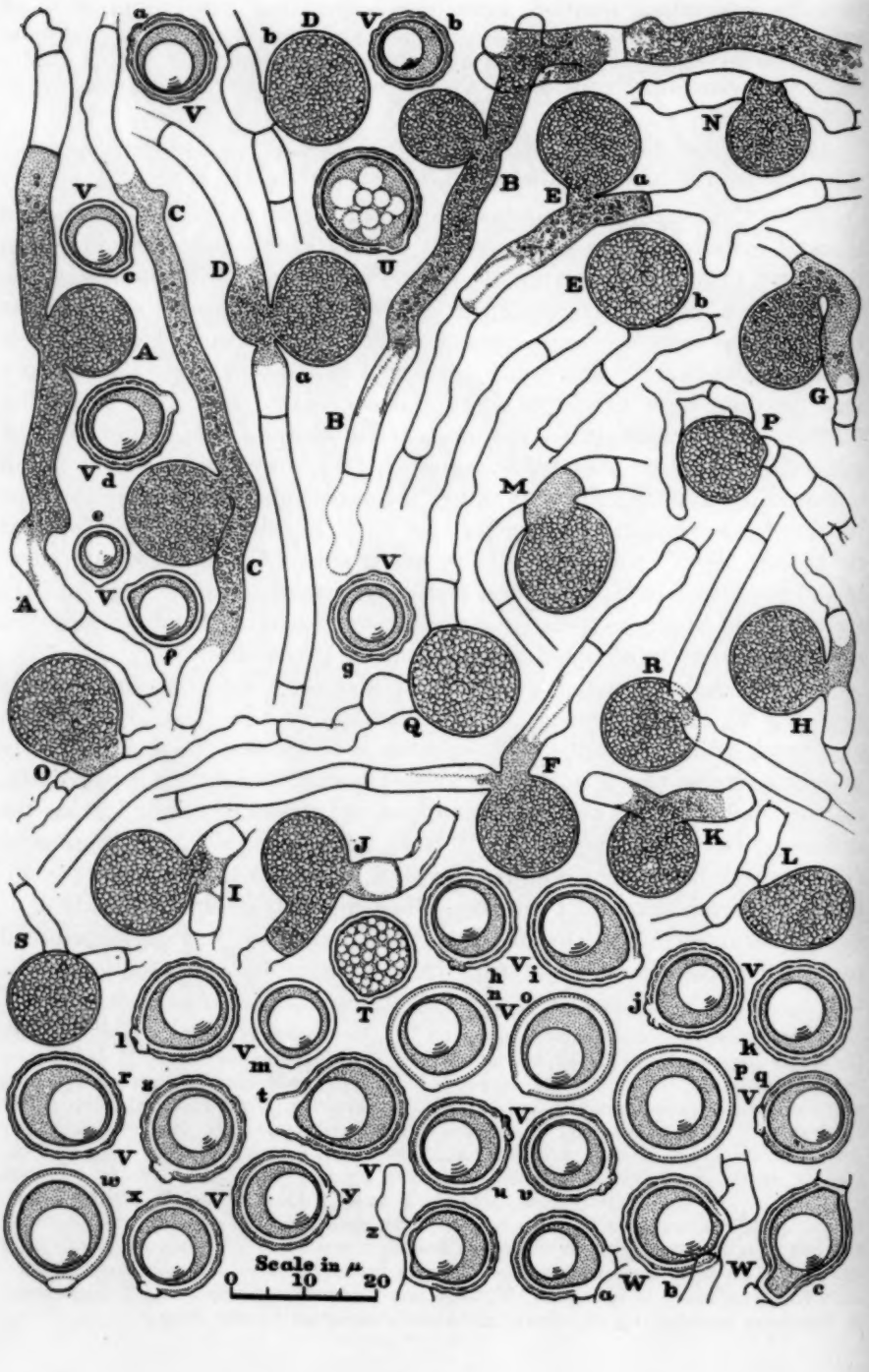
laterally intercalary position, sometimes originating close to junction of gametangia supplied by 2 separate hyphae, yellowish when mature, globose or ellipsoidal, mostly 8 to 17 μ in diameter, surrounded by a wall .7 to 2 μ thick that commonly consists of a smooth inner layer and an undulated outer layer.

Isolated from decaying leaves of deciduous trees (mainly *Quercus* spp.) collected near Starkville, Mississippi, on September 11, 1956.

When *Conidiobolus undulatus* has grown for 20 to 30 days in slanted tubes of maizemeal agar the fungus is plainly visible to the naked eye in the rather opaque upper layer of substratum as well as in the whitish accumulation of conidia overlying the lower half of the slanted surface. The fungus is less conspicuous in maizemeal-agar plate cultures 5 days old, its presence here being most readily noticeable in dappled areas where many small mycelia have developed from globose conidia that after springing forcibly off the conidiophores fell in scattered positions on unoccupied moist substratum. On microscopical examination the growing mycelia are found to consist of hyphae following rather crooked courses and terminating at the margin in elongating segments (fig. 3, A, B) about 5 μ wide; so that the species, like *C. paulus*, may be reckoned among the most delicate members of the genus. In older cultures markedly narrower hyphae (fig. 3, C, D) are produced through vegetative germination of conidia that have fallen on substratum already occupied by mycelium of the fungus.

In both their formative (fig. 3, E-I) and their more advanced stages (fig. 3, J-N) of development the conidiophores of *Conidiobolus undulatus* have much similarity to the conidiophores of *C. paulus*, though apparently in some instances (fig. 3, J, L) they project farther into the air. Apparently, too, their phototropic aerial terminations, in widening upward from the surface of the substratum (fig. 3, E-N:s), more often attain their greatest diameter well below the conidium (fig. 3, E, G, H, K) than the corresponding aerial terminations of *C. paulus*. When the fully delimited conidium of *C. undulatus* springs off its distally widened support, it acquires a broad papilla that merges smoothly with its globose contour. Consequently the

FIG. 3. *Conidiobolus undulatus* as found in maizemeal-agar cultures; ×1000. A, B, Distal portions of two main hyphae at margin of a growing mycelium. C, D, Slender hyphal segments from a culture 24 days old. E-H, Four conidiophores, each arising from a procumbent hyphal segment; s, surface of substratum. I-K, Terminal portions of three conidiophores originating from submerged hyphal segments and bearing partly delimited conidia; s, surface of substratum. L-N, Distal portions of three conidiophores, each of which arises from a submerged hyphal segment and bears a fully delimited conidium; s, surface of substratum. O (a-z), P (a-k), Detached conidia showing variations in size and shape. Q, R, Two conidia, each giving rise to a secondary conidium. S, T, Two conidia, each with an outgrowth bearing a secondary conidium ready to spring off. U, V, Two conidia, each with a germ hypha that terminates as a conidiophore bearing a conidium ready to spring off. W, Conidium germinating in unoccupied substratum. X, Conidium germinating on substratum already occupied by the fungus.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0 10 20

detached conidia (fig. 3, O, a-z; P, a-k) resemble those of *C. paulus* in their rather smoothly obovoid shape as well as in their small dimensions and somewhat densely granular contents. Many detached conidia push up a broad outgrowth on which a secondary globose conidium is formed (fig. 3, Q-T). Others emit a germ hypha, which, after elongating procumbently a short distance, abruptly grows upward as a phototropic conidiophore whereon likewise a secondary globose conidium is borne (fig. 3, U, V). Germ hyphae extended from conidia lying on fresh substratum (fig. 3, W) are commonly wider than those given off by conidia lying on substratum already occupied by the fungus (fig. 3, X).

In maizemeal agar cultures *Conidiobolus undulatus* produces zygospores abundantly. Especially in the earlier stages sexual reproduction proceeds much as in *C. paulus*, the young zygospore nearly always budding forth laterally (fig. 4, A-S) near the junction of the paired gametangia. Since this junction often appears as a constriction (fig. 4, A; B; D, a; F; I; J) it may be inferred that apical conjugation between separate hyphal branches is fairly common. Yet rather often, again, the 2 hyphal arms supplying the growing zygospore show no marked constriction; so that more often than in *C. paulus* the reproductive unit either presents the appearance of having originated from adjacent segments of the same hypha (fig. 4, C, G, H, K, O) or provides no clear indication as to the manner of its origin (fig. 4, E, a; L-N; P-S). In many instances the full-grown zygospore is found delimited by a single basal septum as a globose body sessile on the empty membrane of one of the gametangia (fig. 4, D, b; E, b; L). More often than in *C. paulus* it is delimited by a septum from each empty gametangium, and then appears in laterally intercalary relation to the tubular envelopes of the parent segments (fig. 4, M-S). While the typically lateral or laterally intercalary position of the zygospore is somewhat unusual, being found among known congeneric forms only in *C. paulus*, the earlier stages of sexual reproduction in *C. undulatus*, as in many other members of the genus, are so lacking in distinctiveness that they might readily be mistaken for stages in chlamydospore formation.

Close parallelism with development in congeneric species is likewise shown in the reorganization of contents entailed in maturation of the zygospores. The small globules distributed through the newly delimited subspherical cell (fig. 4, P-S) coalesce to form globules of increasing size (fig.

FIG. 4. *Conidiobolus undulatus* as found in maizemeal-agar cultures; ×1000. A-C, Three sexual reproductive units, each with zygospore in active growth. D, E, Two sexual reproductive units, each showing: a, zygospore in advanced stage of growth; b, zygospore newly delimited 30 minutes later. F-K, Six sexual reproductive units, each showing zygospore in late stage of growth. L, Lateral zygospore newly delimited. M-S, Seven newly delimited laterally intercalary zygospores. T, U, Two slightly immature zygospores having plural globules. V (a-z), W (a-e), Mature zygospores showing variations in size and shape.

4, T, U) until at full maturity only a single large globule is found surrounded by protoplasm of nearly homogeneous appearance (fig. 4, V, a-z; W, a-e). While the internal changes are taking place the enveloping wall gains in thickness. If many thousands of ripe zygospores in a maizemeal-agar culture are examined, a few undersized specimens can usually be found in which the thickened wall is smooth and consists apparently of a single layer (fig. 4, V, c, e, f, m). Diligent search in some cultures may uncover also a few specimens of normal size that closely resemble the zygospores of *Conidiobolus paulus* in being surrounded by a smooth wall in which a thin outer layer, presumably corresponding to the membrane of the newly delimited fusion cell, is everywhere adnate to a thicker inner layer (fig. 4, V, n-p, w). However, owing to the undulate sculpture generally characteristic of the mature zygospores (fig. 4, V, a, b, d, g-l, q-v, x-z; W, a-e), cultures in which sexual reproduction has proceeded for several days show far more conspicuous similarity to *C. rugosus* Drechsler (1955 b) than to any other species. The similarity in sculpture derives mainly from similar differentiation of the zygospore wall into a wrinkled outer layer and a smooth inner layer. In its structure the zygospore wall of *C. undulatus* as well as of *C. rugosus* would seem to agree broadly with that of *Basidiobolus ranarum* Eidam (1886).

Conidiobolus undulatus differs from *C. rugosus* in its narrower mycelial hyphae and in the smaller dimensions of its conidia and zygospores. Its conidia, moreover, show less distinct demarcation of the basal papilla than those of *C. rugosus*. While the zygospores of *C. undulatus* are usually borne in lateral or laterally intercalary position and only rarely can be observed in mesially intercalary position, those of *C. rugosus* commonly develop intercalarily in axial alignment with the parent hyphal segments. The zygospores of *C. undulatus* usually show only faint yellowish coloration, whereas those of *C. rugosus* are distinguished by the most pronounced yellow coloration hitherto seen in any member of the genus.

PLANT INDUSTRY STATION
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A REVISION OF THE GENUS LESCURAEA IN EUROPE AND NORTH AMERICA

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Lescuraea is one of seven genera in the Leskeoideae subfamily of the Leskeaceae. Our knowledge of members of the genus goes back to 1790 when Jacob Dickson wrote brief descriptions of *Hypnum atrovirens,* the species we now call *Lescuraea patens,* and of *Hypnum filamentosum* which Hedwig later described as *Leskea incurvata.* In 1801 Bridel gave a full description of *Hypnum mutabile* and before 1807 Schleicher distributed specimens of *Hypnum plicatum* collected in Switzerland. In 1828 Drummond distributed his *Hypnum tenax* collected in British Columbia; it contained the two mosses which Wilson called *Hypnum congestum* and *Leskea rigescens.*

The genus *Lescuraea* was described by Bruch, Schimper and Guembel in 1851 for the species with erect capsules; it included *L. striata* with the variety *saxicola* and *L. rigescens* of Wilson. In 1852 the same authors described the genus *Pseudoleskea* for the species with curved asymmetric capsules, *P. atrovirens, P. catenulata, P. congesta,* and *P. Liebmanii* (*Rauia subcatenulata*). In 1860 Schimper described the genus *Ptychodium* for a species with strongly plicate leaves, *P. plicatum.*

Lindberg (1871) revised the spelling of *Lescuraea* to *Lesquereuxia,* and in 1879 he listed under this genus all the species known to occur in Scandinavia, namely, *L. filamentosa, L. saxicola,* and *L. plicata.* In 1895 Limpricht followed Schimper in retaining the three generic names, but with the species distributed as follows: *Lescuraea striata* and *L. saxicola; Pseudoleskea patens* and *P. atrovirens; Ptychodium plicatum, P. Pfundtneri, P. oligocladum* and *P. decipiens.* Kindberg in 1896 retained the genus *Lescuraea* but united *Pseudoleskea* and *Ptychodium* under the name *Pseudoleskea.* In 1910 Arnell and Jensen united all the species under *Lescuraea* except *Ptychodium plicatum.* Brotherus (1923) followed the same plan as Kindberg with the two genera, *Lescuraea* and *Pseudoleskea.* In 1927 Moenkemeyer returned to the system used by Lindberg and by Arnell and Jensen placing all the species except *Ptychodium plicatum* in *Lescuraea* and using the original spelling of Bruch, Schimper and Guembel. Moenkemeyer and Brotherus (1925) placed *Ptychodium plicatum* in the Rhytidiaceae following a system devised by Fleischer (1922).

In 1925 Brotherus divided *Pseudoleskea* into three sections, Pseudo-Pterogonium, Eu-Pseudoleskea and Orthotheciella. On the basis of the structure of the capsules which were unknown previously, Reimers (1926) assigned the Orthotheciella section to the Amblystegiaceae. In 1929 Thériot

showed very clearly that the Pseudo-Pterogonium section belongs to the genus *Pseudoleskeopsis*; this genus differs from *Lescuraea* and from *Pseudoleskea* in being monoicous, in having well developed cilia and in respect to the papillae and paraphyllia which are lacking or very poorly developed.

In the present work the older name *Lescuraea* is used with the spelling of Bruch, Schimper and Guembel, and *Pseudoleskea* and *Ptychodium* become synonyms. The generic name *Lesquereuxia* has been associated with species from Japan since 1872 when Lindberg described *L. robusta* which lacks papillae and paraphyllia and differs radically in the structure of the peristome.

Lescuraea, Leskeella and *Pseudoleskeella* are dioicous, a character which distinguishes them from the other genera of the subfamily. The species assigned by Brotherus (1925) to *Leskeella* and *Pseudoleskeella*, respectively, have been variously distributed by different authors. For example, *P. catenulata* has been put in the genus *Pseudoleskea* by some bryologists where it is clearly out of place.

Lescuraea can be distinguished from *Leskeella* and from *Pseudoleskeella* as follows: *Lescuraea* consists of small to large plants, with paraphyllia numerous except in *L. baileyi* and *L. iliamniana*, alar cells predominantly quadrate except in *L. incurvata* where both quadrate cells and transversely elongate cells are common, peristome teeth united at base to form a conspicuous dark brown band in subgenera *Pseudoleskea* and *Tricholeskea* and an inconspicuous yellow to brown band in subgenus *Lescuraea;* in *Leskeella* and *Pseudoleskeella* the plants are all small, with paraphyllia lacking or very few, alar cells a conspicuous group with transversely elongate cells predominant, peristome without a dark band at base. Thus the structure of the alar cells will distinguish *Leskeella* and *Pseudoleskeella* from all members of *Lescuraea* except *L. incurvata;* but *L. incurvata* has abundant paraphyllia on the stems, while paraphyllia are wanting or very few in the two related genera.

Lescuraea as defined below contains approximately seventeen species, eleven of which are found in Europe and North America. Of the nineteen taxa treated here, holotypes or isotypes were studied for all except five, and specimens cited by Limpricht (1895) were available for four of the ones where the types were lacking; for the *jemtlandica* form of *L. radicosa* a specimen from the type locality was studied. Seven types are in the herbarium of the New York Botanical Garden, three in the herbarium at Riksmuseum in Stockholm, and two in the Lausanne herbarium. In addition, the type specimens were studied for many of the plants whose names appear as synonyms. Several thousand specimens were examined in the course of the study but only a part of them appear in the citations. The author is especially grateful to the curators of the herbaria which supplied

the types and to the University of Washington where a part of the work was done.

The following abbreviations designate the location of specimens cited below and the writer wishes to thank all institutions and individuals for material which was loaned:

ARIZ	University of Arizona, Tucson, Arizona.
CAN	National Museum of Canada, Ottawa, Canada.
COLO	The University of Colorado, Boulder, Colorado.
CU	Cornell University, Ithaca, New York.
DUKE	Duke University Herbarium and the Herbarium of the American Bryological Society, Durham, North Carolina.
IA	Herbarium of H. S. Conard, State University of Iowa, Iowa City, Iowa.
LAWTON	Herbarium of Elva Lawton, Hunter College, New York 21, N.Y.
LAU	Musée Botanique Cantonal, Lausanne, Switzerland.
MICH	University of Michigan, Ann Arbor, Michigan.
MO	Missouri Botanical Garden, St. Louis, Missouri.
NY	New York Botanical Garden, New York 58, N.Y.
PC	Muséum d'Historie Naturelle, Laboratorie de Cryptogamie, Paris, France.
S-PA	Naturhistoriska Riksmuseum, Paleobotanical Dept., Stockholm, Sweden.
UARK	University of Arkansas, Fayetteville, Arkansas.
US	National Museum, Smithsonian Institution, Washington, D.C.
UT-F	Herbarium of S. Flowers, Univ. of Utah, Salt Lake City, Utah.
WTU	University of Washington, Seattle, Washington.

Lescuraea B.S.G. Bryol. Eur. fasc. 46–47. 1851, emend. Moenkem. Die Laubm. Eur. 689. 1927.

Pseudoleskea B.S.G. Bryol. Eur. fasc. 49–51. 1852.

Ptychodium Schimp. Syn. Musc. Eur. 527. 1860.

Plants small to large but mostly medium sized, green to yellow green or brownish when old; stems prostrate, elongate, usually branched, central strand present or wanting but never well developed; branches arranged irregularly, often hooked at tips, never flagelliform; rhizoids usually present in tufts, normally unbranched, rare in a few species; paraphyllia numerous except in *L. baileyi* and *L. iliamniana*, filamentous or lanceolate, entire or with a few teeth, unbranched, not papillose. Leaves ovate or ovate-lanceolate, those on the stems mostly a millimeter or more long, rarely less, but reaching three millimeters in some species, falcate and asymmetric or straight and symmetric, plicate, decurrent; margin generally more or less recurved, often serrulate especially at tips of branch leaves; costa single, usually ending below apex but percurrent or nearly so in a few species. Alar cells predominantly quadrate but in some species transversely elongate in part; median cells varying from isodiametric to linear; cell

walls thin or thick, pitted in some species. Papillae present in many species especially at tips of branch leaves, one per cell or one on each surface of cell, either consisting of the projecting ends of cell walls or formed on surface of cell wall and located centrally or nearer upper end.

Plants dioicous, male and female plants similar; sex organs borne on main stems, paraphyses usually present; perigonial bracts short, deeply concave, midrib faint or wanting, antheridia several; perichaetial bracts acuminate from an elongate base, usually with a midrib, but midrib sometimes faint or lacking. Seta elongate, smooth, usually twisted, of the same reddish brown color as the capsule; calyptra cucullate, falling early; capsule erect and symmetric or inclined to horizontal and asymmetric, with inconspicuous rudimentary stomata at base; operculum conic or with a very short beak; true annulus never formed, but cells at junction of urn and operculum somewhat differentiated and adhering to either. Peristome double; the sixteen teeth of the exostome either with well developed lamellae and with fine horizontal lines at base, or less well developed and without lamellae and fine lines, yellow to yellow brown, united at base for a distance of one to six joints to form a yellow to dark reddish brown band, the band inserted below the mouth of the capsule to the light colored thin walled cells of the inner capsule wall; endostome variable, with basal membrane very narrow or to half the length of the teeth; segments sixteen, broad and keeled or narrowly linear, from nearly as long as exostome to quite short; cilia usually rudimentary or wanting, but occasionally well developed; in a few species with poorly developed peristomes the endostome may be somewhat adherent to the columella or to the teeth; spores usually rough, 10–22 μ.

Type species, *Pterogonium striatum* Schwaeger.

Found in cold regions on rocks or trees, rarely on the ground.

Three groups of species can be recognized in *Lescuraea* as treated here, but some species are intermediate in character and for this reason the divisions are called subgenera and not genera. The differences most commonly given to separate these species into genera have been erect capsules in contrast to curved capsules, the presence or absence of lamellae on the peristome teeth, segments of the endostome keeled or not keeled, the presence or absence of a central strand in the stem and the length of the leaf cells. The teeth of *L. iliamniana* have lamellae but other characters show a definite relationship to the species without lamellae. The segments of the endostome of *L. stenophylla* are narrow and not keeled but in all other important characters this species resembles the group with keeled segments. Limpricht (1895) believed that the central strand in the stem was important in separating his genera, but Loeske (1911) showed very clearly that this is not a reliable character, for the central strand may be quite evident in the older part of a stem and faint or lacking in the younger part of the same stem. The fundamental cell structure of the leaves is important in distinguishing subgenera and species but more than cell length is involved.

In the keys and in the descriptions which follow, all references to size

of median cells mean cells of stem leaves between the midrib and margin about one third to half way above leaf base. Unless otherwise stated always look for papillae on tips of branch leaves, or if branches are wanting, on tips of young stem leaves. Papillae may be present on older leaves and below the leaf tips, but they are easier to find in the places indicated.

KEY TO THE SUBGENERA OF LESCURAEA

1. Basal cells of stem leaves not longer than median cells; paraphyllia numerous except in *L. iliamniana*; leaves without hair points.
   2. Peristome teeth united at base to form a conspicuous dark brown band; teeth with lamellae; segments plainly keeled except in *L. stenophylla* ..... A. Subgenus *Pseudoleskea.*
   2. Peristome teeth united at base to form a narrow inconspicuous band which is yellow to brown; teeth without lamellae except in *L. iliamniana*; segments never keeled ..... C. Subgenus *Lescuraea.*
1. Basal cells of stem leaves (except alar) longer than median cells; paraphyllia wanting; leaves with hyaline hair points ..... B. Subgenus *Tricholeskea.*

ARTIFICIAL KEY TO THE SPECIES OF LESCURAEA

1. Leaf cells with large papillae on faces of cells, usually central. 1. *L. patens.*
1. Leaf cells with small papillae at cell ends or papillae wanting.
   2. Paraphyllia very few or none.
      3. Basal cells (except alar) longer than median cells ..... 8. *L. baileyi.*
      3. Basal cells shorter than median cells ..... 11. *L. iliamniana.*
   2. Paraphyllia abundant at least on stems.
      4. Cells of mature stem leaves plainly pitted ..... 5. *L. atricha.*
      4. Cells of stem leaves not pitted or with pits in basal cell only.
         5. Stem leaves 2.5 mm. long or longer, strongly plicate; basal cells (except alar) plainly pitted ..... 7. *L. plicata.*
         5. Stem leaves without this combination of characters.
            6. Leaves large, 1.7–2.3 × 0.7–1.0 mm.; branches and rhizoids few or none.
               7. Cell walls thick; median cells mostly 12–20 μ long, rarely a few to 30 μ ..... 2. *L. incurvata* var. *gigantea.*
               7. Cell walls thin; median cells mostly 30 μ long or longer ..... 4. *L. radicosa* var. *denudata.*
            6. Leaves smaller; branches and rhizoids common.
               8. Basal cells of stem leaves (except alar) predominantly long with many cells more than twice as long as wide.
                  9. Leaves abruptly acuminate with a narrow oblique acumen, strongly revolute at base of acumen; branch leaves strongly papillose ..... 3. *L. saviana.*
                  9. Leaves otherwise.
                     10. Branch leaves smooth and entire; plants growing on trees ..... 9. *L. striata.*
                     10. Branch leaves papillose and serrulate; plants growing on rocks ..... 10. *L. saxicola.*
               8. Basal cells of stem leaves predominantly short, 1:1 or 2:1.
                  11. Median cells of stem leaves less than 2:1. 2. *L. incurvata.*
                  11. Median cells of stem leaves 2:1 or longer.
                     12. Alar cells of stem leaves in part quad-

rate and in part tranversely elongate; median cells mostly 12–20 μ long, if longer the walls very thick and short cells intermingled ..... 2. *L. incurvata.*

12. Alar cells of stem leaves quadrate; median cells of stem leaves commonly longer than 20 μ, often 30 μ or more; if shorter the walls not conspicuously thickened.

13. Leaves gradually long acuminate with acumen more than half the length of leaf; cells usually papillose, the papilla over cell cavity at upper end; segments of endostome narrow and not keeled ..... 6. *L. stenophylla.*

13. Leaves with a shorter acumen; papillae when present always formed by projecting ends of cell walls; segments broad and keeled.

14. Leaves abruptly acuminate with a narrow oblique acumen, strongly revolute at base of acumen; branch leaves strongly papillose. ..... 3. *L. saviana.*

14. Leaves without this combination of characters.

15. Leaves plainly acuminate; apical cells long, mostly 30 μ or more ..... 4. *L. radicosa* var. *radicosa.*

15. Leaves merely acute or with short acumen; apical cells short, less than 30 μ.

16. Branch leaves strongly concave; leaves a clear light green ..... 4. *L. radicosa* var. *pallida.*

16. Branch leaves not strongly concave; leaves yellow green to brownish 4. *L. radicosa* var. *compacta.*

A. Subgenus *Pseudoleskea* (B.S.G.) Lesq. & James, Man. Mosses N. Am. 319. 1884.

Eu-Pseudoleskea Kindb. Eur. & N. Am. Bryin. 49. 1896.

Section *Eu-Pseudoleskea* Broth. in Engler & Prantl, Nat. Pfl. 1(3): 1000. 1907.

Plants small to large, paraphyllia numerous, leaves without hair points; basal cells of stem leaves not longer than median; median cells variable, isodiametric to linear; leaves frequently papillose. Capsules curved and asymmetric or erect and symmetric; peristome teeth united at base to form a conspicuous dark band, lamellae and fine horizontal lines always present;

segments of endostome keeled except in *L. stenophylla*; cilia from well developed to rudimentary or wanting.

Type species, *Leskea incurvata* Hedw.

This subgenus is large and to some bryologists may appear to be composed of distinct groups, but further division is unsatisfactory. It consists of species which are apparently in the process of evolution, and while typical specimens are quite distinct, others may be intermediate.

1. *Lescuraea patens* (Lindb.) Arn. & Jens. Naturwiss. Untersuch. Sarekgeb. Schwed.-Lappl. 3: 212–213. 1910.

Leskea (?) *patens* Lindb. Medd. Soc. Fauna Fl. Fenn. (9 Oct. 1880) 6: 251. 1881 (nomen nudum).

Lesquereuxia patens Lindb. Medd. Soc. Fauna Fl. Fenn. 14: 75–77. 1887.

Pseudoleskea atrovirens var. *patens* Hagen in sched. 1894.

Pseudoleskea patens Limpr. Die Laubm. 2: 806–808. 1895.

Pseudoleskea heterocladioides Kindb. Revue Bryol. 22: 83. 1895.

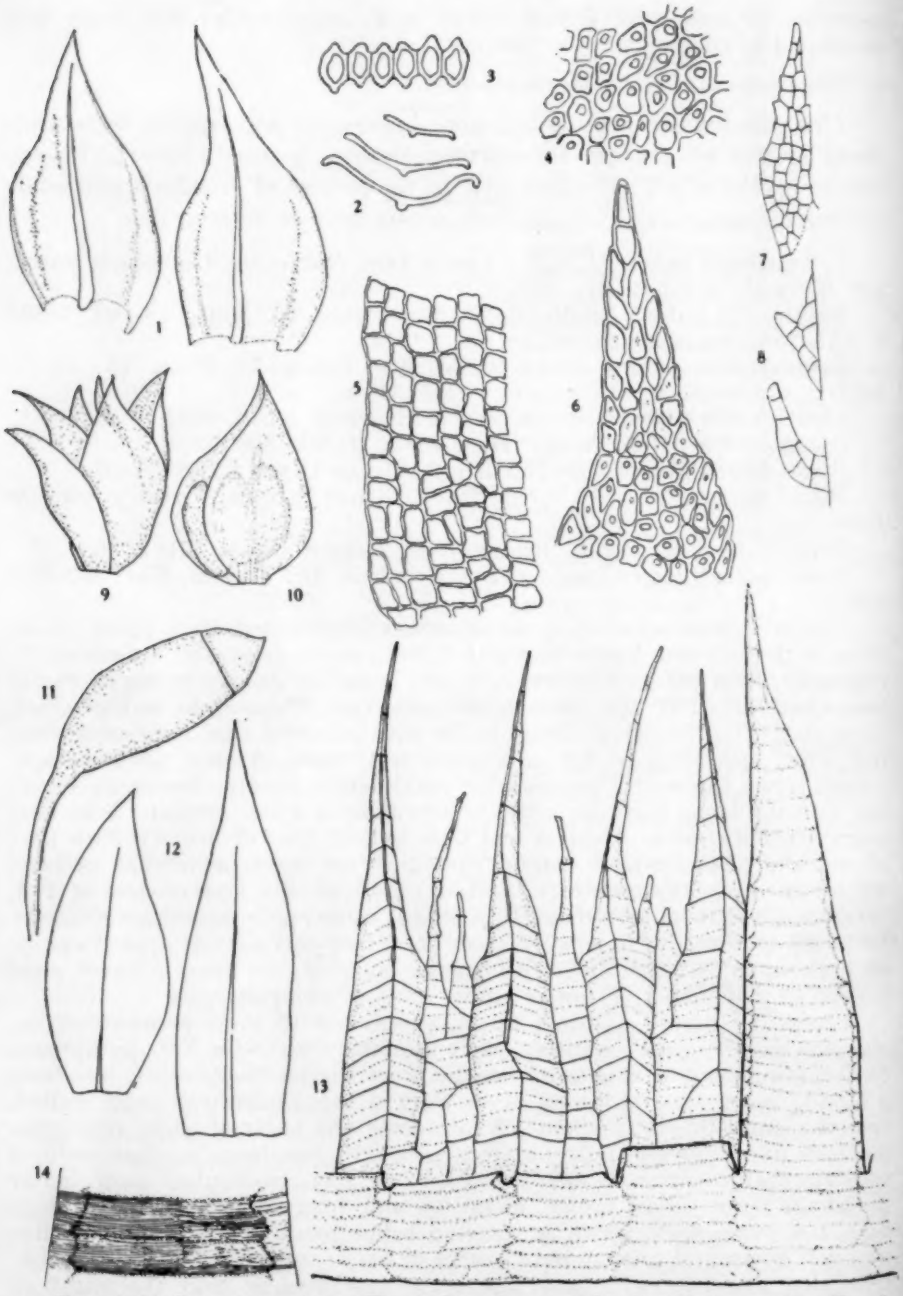
Pseudoleskea atrovirens subsp. *tenella* Kindb. Eur. & N. Am. Bryin. 50. 1896.

Lesquereuxia atrovirens Braith. Brit. Moss Flora 3: 121. 1900.

Lescuraea atrovirens var. *patens* Moenkem. Die Laubm. Eur. 692–693. 1927.

Plants in mats which may be somewhat intertwined, dark green above, often with yellowish tinge, brownish below; stems prostrate, branching irregularly, with tufts of brown rhizoids; branches usually straight, rarely somewhat curved at tips; paraphyllia numerous, filamentous or lanceolate, large ones often decurrent. Stem leaves with incurved tips, appressed when dry, erect spreading on all sides when wet, ovate at base, acute to acuminate, from symmetric to somewhat asymmetric, plicate, decurrent, reaching 1.2×0.5 mm.; margins entire or serrulate at apex, revolute from base nearly to apex, or revolute at leaf base and at base of acumen with part of margin plane; midrib strong, ending below apex, somewhat pellucid when dry; alar cells quadrate; median cells typically isodiametric or 2:1, rarely somewhat longer, about 10 μ broad; apical cells sometimes elongate. Branch leaves similar or smaller, more frequenty serrulate at apex. Papillae on both surfaces, large and conspicuous, especially on branch leaves, over middle of cell lumen or nearer upper ends of elongate cells.

Perigonial bracts clasping, broad, concave, with short acumen, entire, margins plane, midrib wanting, cells smooth; antheridia 5–8, paraphyses filamentous, about as long as antheridia. Perichaetial bracts acuminate from a broad base, costate but costa often weak at base; cells long, thick walled, smooth; inner bracts to about 1.8 mm. long, the outer shorter; short filamentous paraphyses usually present. Seta 7–15 mm. long; capsule inclined to horizontal, asymmetric, urn about 1.5×0.8 mm.; operculum conic; outer peristome teeth yellow brown, about 0.5 mm. long, united to form a dark base 4–6 joints wide which is inserted below mouth of capsule; lamellae and fine horizontal lines present except at apex; inner peristome yellowish, somewhat papillose, with basal membrane one third or more the length of endostome; segments nearly as long as teeth, open on keel; cilia one or two, poorly developed or none; spores 14–18 μ. (figs. 1–14).



FIGS. 1–14. *Lescuraea patens*. FIG. 1. Stem leaves of Lindberg's type. ×38. FIG. 2. Leaves in cross section. ×38. FIG. 3. Cross section of median leaf cells to show papillae. ×360. FIGS. 4, 5 and 6. Median, alar and apical cells of leaf. ×360. FIGS. 7 and 8. Paraphyllia. ×150. FIG. 9. Perigonium. ×38. FIG. 10. Perigonial bract with antheridia. ×38. FIG. 11. Capsule. ×14. FIG. 12. Perichaetial bracts. ×38. FIG. 13. Part of peristome. ×175. FIG. 14. Part of an outer tooth near base. ×360.

Type: Sweden, Lindberg s.n. (holotype S-PA!).

On rocks in alpine regions, rarely at low elevations in the north. Alaska, British Columbia, Washington, Oregon, California, Montana, Idaho, Wyoming, Utah, Nevada, Michigan, Nova Scotia, Newfoundland, New Hampshire, Scotland, Sweden, Norway, Iceland, and throughout the mountains of southern Europe.

Illustrations: Limpr. (1895) f. 349; Braith. (1900) pl. 107 E; Best (1900) pl. 7, f. 1–7; Sharp (1934) pl. 53, f. 1–7.

Representative specimens examined: Alaska: Yakutat Bay, Trelease and Saunders, June 21, 1899, Harriman Exp. 1746a (NY); Kodiak Island, Olga Bay, Mt. Bench at 200 ft. Loof, June 1940 (S-PA); Juneau, Mehner May 1904 (NY, CAN). British Columbia: Bear Lake, Zineton, McFadden, May 13, 1926 (IA, MICH, CAN). Alberta: Cameron Lake, Crum and Schofield 5722 (CAN). Washington: Mt. Rainier along Tahoma Creek, Frye 90 (WTU, NY, MICH, IA); Jefferson Co., Olympic Peninsula, Queets River Valley near Humes Glacier, Frye, Aug. 14, 1907 (WTU). Oregon: Klamath Co., Crater Lake National Park, Sun Creek Valley, Frye, July 14, 1933 (WTU, LAWTON). California: Sequoia National Park, Halstead Trail, Degener 16939 (NY); Eldorado Co., Echo Lake, Conard, Sept. 5, 1947 (IA); Placer Co., Flume below Emigrant Gap, McFadden, July 9, 1934 (DUKE, NY, CAN); Tuolumne Co., Sonora Pass Road, Wiggins, July 31, 1938 (CAN). Montana: Glacier Co., Glacier National Park, Lawton 1214 (LAWTON). Idaho: Kootenai Co., Sandberg, Feb. 13, 1899 (NY), Leiberg, 1892 (NY). Utah: Salt Lake Co., Lamb's Canyon, Flowers 1663, 1691 (UT-F). Nevada: Ormsby Co., Sierra Nevada Mts., Lake Tahoe, Lawton 3123 (WTU). Wyoming: Carbon Co., Medicine Bow Mts., French Creek, Lawton 1689 (LAWTON). Michigan; Keweenaw Co., Copper Harbor, Conard, Aug. 31, 1937 (IA). Newfoundland: Deer Lake, Bay Islands, Waghorne, Sept. 2, 1885 (NY). Nova Scotia: Inverness Co., upper Margara River, Erskine 2039 (CU). New Hampshire: White Mountains, Tuckerman's Ravine, Edwin Faxon, July 18, 1884, in packet with *L. radicosa* (NY). Scotland: Perthshire, Ben Lawers, Greville, the specimen sent by Best to the British Museum to be checked with Dickson's type of *H. atrovirens* (NY). Iceland: Grímsey near Holatjorn, Jones, July 1934 issued by Br. Bry. Soc. 485 (MICH). Sweden: Vestergöthland, Mt. Alleberg, Lindberg, June 28, 1880 (holotype S-PA), Norstedt, July 30, 1887 (S-PA), Arnell, July 1887 issued as Husnot, Musci Gall. 835 (S-PA, LAU). Norway: Trondhjems, Hagen, Apr. 20, 1894 (S-PA, CAN). Switzerland: St. Gothard en Airolo, Bottini, July 17, 1887 (LAU). Italy: Prov: Aemilia, Modena Apeninen, Bottini, Aug. 23, 1913 issued by Bauer, Musci Eur. 1228 (NY). Corse: Haute vállee de la Bestonica au Lac de Melo, Camus, June 11, 1901 (PC).

This species is the easiest to recognize and can be distinguished from all others in the genus by the short cells with the large papillae over the lumen on both sides of the lamina.

The first name given to the species was *Hypnum atrovirens* in 1790 by Jacob Dickson for a specimen from Scotland collected by Greville, but because his description was inadequate the name was wrongly applied to the plant later described by Hedwig (1801) as *Leskea incurvata*. Both

species are found on Ben Lawers in Scotland, but *L. incurvata* is the more common. Best (1900) was the first to point out that two plants were to be found under the name *P. atrovirens*, and he sent the two specimens from the herbarium of the New York Botanical Garden to Mr. Gepp at the British Museum to have them checked with the type of Dickson's *H. atrovirens*. The plant which was found to correspond to the type is at the New York Botanical Garden with Best's notation and it is cited above. As a result of Best's work on the genus, American plants with the large central papillae were called *P. atrovirens*, while in Europe this name was applied to the plants with papillae at the ends of the cells. With the adoption of Hedwig's Species Muscorum (1801) as the starting point for nomenclature, the name for the moss with the large central papillae became *L. patens* and the name for the one with the papillae at the cell ends is *L. incurvata*.

In 1933 Amann described the variety *brevifolia* with short, obtuse, entire leaves, and he credits Moenkemeyer with the form *latifolia*, which is large, strongly papillose and with a strongly revolute margin. The species is variable and similar variations have been observed by many bryologists, but they do not seem to be important enough to be named.

2. **Lescuraea incurvata** (Hedw.) comb. nov.

Leskea incurvata Hedw. Sp. Musc. 216. 1801.

Hypnum atrovirens sensu Smith, Fl. Brit. 1307. 1804. (non Dicks.)

Hypnum filamentosum Smith, Fl. Brit. 1308. 1804.

Hypnum incurvum Pal. de Beauv. Prodr. 65. 1805.

Leskea atrovirens sensu Hartm. Skand. Fl. ed. 5. 337. 1849. (non Dicks.)

Pseudoleskea atrovirens sensu B.S.G. Bryol. Eur. fasc. 49–51. 1852. (non Dicks.)

Lesquereuxia filamentosa Lindb. Musc. Scand. 36. 1879.

Leskea filamentosa Kindb. Laubm. Schwed. Norw. 12. 1883.

Pseudoleskea oligoclada Kindb. in Macoun, Bull. Torrey Club 17: 277. 1890.

Pseudoleskea atrovirens var. *tenella* Limpr. Die Laubm. 2: 811–812. 1895.

Pseudoleskea atrovirens subsp. *filamentosa* Kindb. Eur. & N. Amer. Bryin. 50. 1896.

Pseudoleskea filamentosa Broth. Musci in Engler & Prantl, Nat. Pfl. 1 (3): 1001. 1907.

Lescuraea filamentosa Arn. & Jens. Naturwiss. Untersuch. Sarekgeb. Schwed-Lappl. 3: 212. 1910.

Lescuraea atrovirens sensu Moenkem. Die Laubm. Eur. 692. 1927. (non Dicks.)

Pseudoleskea incurvata Dix. Revue Bryol. Lichénol. 6: 109. 1933.

Plants growing in mats not usually interwoven, yellowish green, becoming brown when old; stems elongate, branching irregularly; brown rhizoids in tufts, but some plants with few or none; branches not usually numerous, tips of stems and branches strongly curved; paraphyllia numerous except on some branches, mostly similar to those of *L. patens*, but often larger and the cells with thicker walls. Stem leaves with ovate base and

short acute apex or long acuminate with acumen as long as or longer than leaf base, falcate secund, asymmetric, plicate, decurrent, 0.8–2.3 × 0.35–0.8 mm.; margin usually serrulate at apex except in old leaves, revolute at leaf base and usually at base of acumen; midrib strong, ending below apex or nearly percurrent; alar cells in part quadrate and in part transversely elongate; median cells usually 10–20 × 6–8 μ, including the wall, but sometimes a few cells reaching 25 or 35 μ in length in old leaves; cells opaque, walls thick, usually quite variable in size and shape with long narrow ones intermingled with short broad ones, angular or more often rounded on ends; basal cells sometimes with a few pits; apical cells about the size of median. Branch leaves similar but usually smaller and more often serrulate and papillose. Papillae common on upper surface and back of midrib near apex, rarely present on both sides of lamina, formed by projecting ends of cell walls.

Reproductive structures similar to those of *L. patens*, except the variable inner perichaetial bracts which are often reduced and resemble broad paraphyses.

This species is quite variable with three varieties which may be distinguished by the following key:

1. Median cells of stem leaves mostly elongate with rounded ends and thick walls; papillose to smooth.
   2. Stem leaves 0.8–1.6 × 0.35–0.7 mm. ..... 2 a. var. *incurvata*.
   2. Stem leaves 1.7–2.3 × 0.7–0.8 mm. ..... 2 b. var. *gigantea*.
1. Median cells of stem leaves short, mostly isodiametric, often angular; strongly papillose ..... 2 c. var. *tenuiretis*.

2 a. *Lescuraea incurvata* var. *incurvata*.

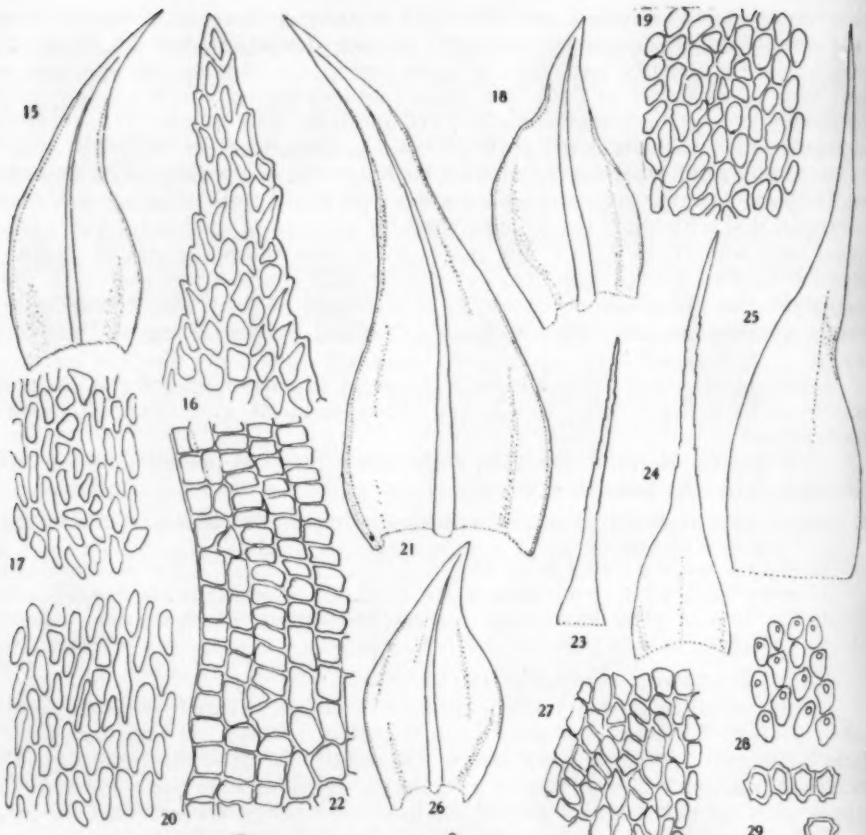
Plants small to medium sized, usually branched; stem leaves commonly 0.8–1.4 × 0.35–0.7 mm., but sometimes reaching 1.6 mm. in length, usually long acuminate, falcate, asymmetric. Median cells of stem leaves mostly elongate but not uniform in size and shape; papillae commonly present on upper surface and back of midrib at least on branch leaves (figs. 15–20).

Type: Sudeten, the mountainous region between Czechoslovakia and Silesia, Germany, not available. Neotype: Limpricht, Bryoth. Sil. 78 (NY!).

On rocks in mountainous regions of British Columbia, Alberta, Washington, Oregon, Montana, Idaho, Wyoming, Nevada, Utah, Colorado, Iceland, and throughout the mountains of Europe.

Illustrations: Hedwig (1801) pl. 53, f. 8–14; Bruch, Schimper & Guembel (1852) pl. 477, f. 1–26; Braith. (1900) pl. 107 D; Best (1900) pl. 7, f. 8–15, pl. 8, f. 25–27; Brotherus (1923) f. 83; Sharp (1934) pl. 53, f. 8–15, 25, 30.

Representative specimens examined:—British Columbia: Vancouver Island, Nanaimo, Mt. Benson, Macoun, June 8, 1887 (type of *P. oligoclada* S-PA, isotype NY); Revelstoke, mouth of Illicillewaet Canyon, Macoun, May 18, 1890, det. by Kindberg as *P. falcicuspis* (US, MICH, CAN, NY). Alberta: Jasper Park, Wilcox Pass, Lawton 1389 (LAWTON). Washington: Kittitas Co., Kachess Lake near Easton, Roell, June 12, 1888 (NY, S-PA); Kittitas Co., Lake Keechelus Valley, J. W. Bailey, July 26, 1916 issued by Grout, N. Am. Muse. Pl. 472 (NY, US, DUKE, IA, S-PA). Oregon: Union Co., Starkey Exp. Range. Weber 3198 (COLO, IA). Montana: Glacier National Park, Logan Pass, Frye, Aug. 24, 1929 (WTU). Wyoming, Teton National Park, east of Teton Pass, Lawton 1783 (LAW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TON). Nevada: Elko Co., Ruby Mts., Thomas Canyon, Lawton 2634 (WTU, LAWTON). Utah: Salt Lake Co., Upper City Creek Canyon, Flowers 1258, 2386 (UT-F). Colorado: within 100 miles of Canyon City, Brandegee, 1874–1878 (NY). Iceland: Dr. Meyer, 1931–1932 (LAU). Scotland: Perthshire, Ben Lawers, Wilson 369 (NY). Norway: Gansta, Jäderholm, July 1895 (S-PA); Dovre, Dr. Kiaer, Rabenhorst, Bryoth. Eur. 991 (NY). Sweden: Lapponia Tornensis, Björkliden, Jäderholm, July 22, 1910 (S-PA); Lapponia Luluensis, Kvikkjokk, Snjarok, E. Nyman, July 20, 1891 (S-PA). Germany: Silesia, Schneegrube, Riesengebirge, Limpricht, Bryoth. Sil. Oct. 1866, 78 (neotype NY); Bohemia, Riesengebirge, Schiffner, Oct. 4, 1899 issued by Bauer, Bry. Boh. 250 (WTU). Austria: Tirol, south side of Kitzbuehler Horn, Crundwell 28, 59 (CAN); Untersberg bei Salzberg, Dr. Schwartz, 1857 in Rabenhorst, Bryoth. Eur. 6, as var. *tenella* (NY, LAU). Hungary: Maramaros prope Korosmezo, Boros, July 18, 1934 (S-PA, LAU). Switzerland: Alpes Vandoises, vallee de Nant, Meylan, Aug 21, 1897 (LAU). France: Haute-Savoie, Forêt des Allamands, Gaume, 1947 (PC). Italy: Prov. Comensis, Alpe Sasso, Valsassine, F. A. Artaria, July 11, 1897, as *P. ticinensis* by Kindberg (S-PA).

The two specimens which follow are somewhat intermediate between variety *incurvata* and variety *gigantea*. Montana: Columbia Falls, Bad Rock Canyon, Williams 256 (NY). Idaho: Traille River Basin, south end of Lake Pend D'Oreille, Leiberg 141, 141a, 141b (NY, US, MICH). Some envelopes of Leiberg 141 contain *L. patens*.

L. incurvata var. *incurvata* has often been confused with *L. radicosa*, but the leaf cells are, on the whole, shorter than in *L. radicosa*. When long cells are present they are narrower than in *L. radicosa* and more opaque. The relative length to width, the cell character frequently used to separate these two species is not a reliable one for some of the long cells of *L. incurvata* have the lumen four times as long as wide, and because the walls of old cells are so thick and the lumen is so narrow the appearance of length is exaggerated.

A comparison of the specimens cited by Limpricht (1895) with the type of Kindberg's *P. oligoclada* has made it perfectly clear that they are one species.

FIGS. 15–29. *Lescuraea incurvata*. FIGS. 15–20. var. *incurvata*. FIG. 15. Stem leaf from type of *P. oligoclada*. ×38. FIGS. 16 and 17. Apical and median cells of stem leaf of type of *P. oligoclada*. ×360. FIG. 18. Stem leaf of Limpricht, Bryol. Sil. 78. ×38. FIG. 19. Median cells of stem leaf, Limpricht 78. ×360. FIG. 20. Median cells of stem leaf of Roell, 1888. ×360. FIGS. 21–25. *L. incurvata* var. *gigantea*, Lawton 2540. FIG. 21. Stem leaf. ×38. FIG. 22. Alar cells. ×360. FIGS. 23–25. Perichaetial bracts from inner to outer. ×38. FIG. 26 and 27. *L. incurvata* var. *tenuiretis* from type. FIG. 26. Stem leaf. ×38. FIG. 27. Median leaf cells. ×360. FIGS. 28 and 29. *L. incurvata*, Becking 5308055, form with papillae on cell lumen. FIG. 28. Cells from acumen of leaf. ×360. FIG. 29. Cross and longitudinal sections of leaf cells to show papillae. ×360. FIGS. 30–35. *L. saviana*, Bauer, Musci Eur. 1226. FIG. 30. Stem leaf. ×38. FIG. 31. Basal cells of stem leaf, midrib to left. ×360. FIG. 32. Median cells of stem leaf. ×360. FIG. 33. Cells of branch leaf near apex showing papillae on revolute margin. ×360. FIG. 34. Capsule. ×14. FIG. 35. Part of inner peristome. ×175.

Limpricht (1895) based his variety *tenella* on a specimen from Austria, Rabenhorst's Bryoth. Eur. 6, which he described as a small form with entire leaves without papillae. The specimen which he cited as the type shows branch leaves with small papillae on the back of the midrib and the leaf margin minutely serrulate in young leaves. It is not sufficiently distinct to be considered a variety.

Boulay (1884) described the variety *filamentosa* as slender and filiform. Slender forms with few paraphyllia on the branches are not uncommon in France, but authentic material has not been available for comparison.

Specimens collected in northern Michigan and reported as *P. oligoclada* are all *L. radicosa*, and no collections of *L. incurvata* from east of the Rocky Mountains have been seen.

2 b. **Lescuraea incurvata** var. **gigantea** var. nov.

Plantae robustiores; caulibus plerumque simplicibus, parce radiculosibus; paraphyllia numerosa. Folia 1.7–2.3 mm. longa, 0.7–0.8 mm. lata.

Plants large with branches and rhizoids few or none; paraphyllia numerous and large; stem leaves 1.7–2.3 × 0.7–0.8 mm., asymmetric, strongly falcate with a broad base and a short or a long acumen; margin slightly to strongly revolute, entire or serrate. Papillae usually present on upper surface and back of midrib in young leaves but often wanting on old leaves (figs. 21–25).

Type: Washington, Lawton 2563 (LAWTON).

On rocks, rarely on decaying wood in Washington, Oregon, Idaho.

Specimens examined:—Washington, Clallam Co., Olympic Peninsula, Elwha River Valley, Trail from Olympic Hot Springs to Boulder Lake, Lawton 2563 (holotype, Lawton), Old Hurricane Road, Lawton 2540 (WTU, LAWTON). Oregon: Umatilla Co., Frazier Creek south of Frazier Ranger Station, Weber 2945 (COLO, IA). Idaho: Latah Co., Moscow Mt., Jones 2079 (IA).

Except for the cell structure which is clearly that of *L. incurvata* this variety resembles *L. radicosa* var. *denudata* and represents a parallel development in form. No European specimens of this variety were seen but no doubt it is to be found there because Brotherus (1925) gave the leaf size for the species as 1.9 × 0.75 mm.

2 c. **Lescuraea incurvata** var. **tenuiretis** (Culmann) comb. nov.

Pseudoleskea filamentosa var. *tenuiretis* Culmann, Revue Bryol. 37: 94. 1910.

This variety differs from variety *incurvata* in having more branches, leaves less falcate, cells short, predominantly isodiametric, usually angular; branch leaves strongly papillose with papillae on both sides of lamina of young leaves (figs. 26 and 27).

Type: Switzerland, Culmann s.n. (holotype LAU!).

On rocks in Switzerland, Germany, Italy, Utah.

Specimens examined:—Switzerland: between Grimsel and Siedelhorn, Culmann, 1908 (holotype LAU). Germany: Riesengebirge, Prager, July 1908, issued as *P. filamentosa* in Bauer, Musci Eur. 1224 (NY, WTU). Italy: Prov. Como, Gipfel des Monte Palanzolo, Artaria, Sept. 6, 1922,

issued as *P. filamentosa* var. *tenella* in Bauer, Musci Eur. 1648 (NY, WTU). Utah: Salt Lake Co., Lamb's Canyon, Flowers 1935 (UT-F).

A form is sometimes found which approaches *L. patens* in the structure and position of the papillae. The cells are isodiametric or elongate, strongly papillose on both sides of the lamina in young leaves; papillae at ends of cells but on lumen and in side view the cavity of the cell can be seen extending into the papilla (figs. 28 and 29); alar cells transversely elongate in part; leaves somewhat falcate and usually asymmetric resembling those of *L. incurvata*. Intermediate forms of this kind suggest the possibility of hybrid origin. Except for the papillae, the cell structure is clearly that of *L. incurvata*. The following specimens have been examined:—Alaska: Yakutat, on rotten log, Stair 4961 (MICH), on rock, Stair 5044 (MICH). Washington: Cascade Mts., on rock, Grant, Aug. 1925 (WTU). Oregon: Clackamas Co., Molalla, on rock, Becking 5308055 (WTU, LAWTON). Norway: Tromso, Arnell, Oct. 7, 1891, determined first as *P. filamentosa* and changed to *L. patens* (S-PA). Scotland: Ben Lawers, Wilson, Aug. 1836 (MICH).

3. **Lescuraea saviana** (De Not.) comb. nov.

Leskea Saviana De Not. Syll. Musc. Ital. 63–64. 1838.

Pseudoleskea illyrica Glowacki, Zool. Bot. Ges. Wien 57: 227–228. 1907.

Pseudoleskea radicosa var. *meridionalis* Culmann in Amann, Culmann & Meylan, Flore Mousses Suisse 2: 285. 1918.

Lescuraea atrovirens var. *Saviana* Moenkem. Die Laubm. Eur. 693. 1927.

Pseudoleskea Saviana Latzel, Beih. Bot. Centr. 48: 490. 1931.

Pseudoleskea filamentosa var. *meridionalis* Culmann in Amann, Flore Mousses Suisse 3: 127. 1933.

Pseudoleskea radicosa ssp. *Saviana* Giacomini, Ann. di Bot. 23: 7. 1945.

Pseudoleskea atrovirens ssp. *atrovirens* var. *illyrica* Giacomini, Atti Inst. Bot. Pavia ser. 5. 4(2): 256. 1947.

Plants in tufts, usually dark green but sometimes brownish; stems prostrate with numerous branches usually hooked at ends; rhizoids in tufts; paraphyllia numerous. filamentous or lanceolate. Stem leaves plainly falcate, abruptly acuminate, asymmetric, plicate, decurrent, 1.2–1.8 × 0.4–0.7 mm., but commonly 1.4 × 0.5 mm.; margin serrulate at apex, revolute, the revolute part especially broad at base of acumen; midrib strong but not reaching apex, rough on back at end; alar cells mostly quadrate; median cells of stem leaves 6–9 μ wide, variable in length but usually 25–35 μ long; basal cells somewhat shorter and broader; cell walls somewhat thickened, sometimes pitted at leaf base. Branch leaves similar but often smaller, strongly papillose on both sides of lamina at apex, the papillae formed by projecting ends of cell walls.

Sex organs and bracts similar to those of *L. patens*. Seta 10–12 mm. long; capsule straight and symmetric but often inclined by the bent seta, the urn about 2 × 0.8 mm.; operculum conic; outer peristome similar to that of *L. patens*; segments keeled, open on keel, cilia lacking; spores 13–16 μ, minutely papillose (figs. 30–35).

Type: Italy, not seen. Isotype in Mitten herbarium, s. n. (NY!).

Usually growing on wood. Common in the mountains of southern Europe, rarely found in America in the state of Washington.

Illustrations:—Moenkem. (1927) f. 155 d; Pilous (1955) pl. 1, f. a–g, pl. 2, f. 1–3.

Representative specimens examined:—Italy: Appenines, Etruria (isotype, NY); Boscolungo in Appenines, Aemilae, E. Levier, May 1880 (LAU). Switzerland: Dolomiti del Gruppo, Langsropel, Kern, July 21, 1899 (LAU). Corsica: Forêt de Vizzavona, Camus, 1901 (PC). Hungary: Heves, montis Kekes prope Parad, Boros, Mar. 25, 1951 (S-PA, LAWTON). Yugoslavia: Krain, Schneeberg bei Laar, Glowacki, July 12, 1910 (S-PA, LAWTON); Hercegovina, Rothbuchenwald between Vrbanje and Orjensattel, Baumgartner, June 1911 issued by Bauer, Musci Eur. 1226 (WTU, NY). Baumgartner 2295 (NY, US, S-PA). Romania: Monti Sabini, Mt. Tarino, Fleischer & Warnstorf, Bry. Eur. 83 (WTU, LAU). Greece: monte Olympo Thessaliae in valle Malta, Handel-Mazetti, July 1927 issued by Verdoorn, Musci Selecti et Critici, ser. 6, 295 (WTU, MICH, NY). Washington: Clallam Co., Olympic Peninsula, trail from Olympic Hot Springs to Boulder Lake, Lawton 2597 (LAWTON).

This species resembles both *L. incurvata* and *L. radicosa* and is intermediate between them in respect to cell size and thickness of cell walls, but differs from both in being more strongly papillose with the papillae on both sides of the lamina. The oblique apex of the leaf, the strongly recurved leaf margin and the symmetric capsules are also important distinguishing characters.

The variety *meridionalis* of Culmann (1918) was first given under *P. radicosa* with the description based on Fleischer and Warnstorf, Bry. Eur. 83, but using the same specimen in 1933 Amann placed the variety under *P. filamentosa* (*incurvata*).

Under *P. atrovirens* Limpricht (1895) gave the variety *brachyclados* with the following synonyms; *Leskea brachyclados* Schwaegr. in Schulte's Reise auf dem Glockner 2: 364, 1804; *Leskea incurvata* var. *brachyclados* Brid. Spec. musc. 2: 81, 1812; *Pseudoleskea atrovirens* var. *brachyclados* B.S.G. Bryol. Eur. fasc. 49–51. 1852. Limpricht described the variety *brachyclados* as having larger leaves than *P. atrovirens*, reaching 1.4×0.7 mm., cells more strongly papillose with the papillae on both sides, basal cells with pitted walls, median cells elongate (2:1) and "S" shaped. Specimens of *L. saviana* fit Limpricht's description in most respects, but the cells are often more than 2:1. Because Limpricht cited no specimens under variety *brachyclados*, it is doubtful whether we can ever know precisely what he meant by his variety.

Both Best (1900) and Culmann (1910) examined specimens from the Schwaegrichen herbarium under the name *brachyclados* and both pronounced them *P. radicosa*, and Culmann expressed the opinion that the name *brachyclados* should be completely abandoned.

De Notaris (1869) gave the variety *brachyclados* as a synonym of *L.*

saviana, and Meylan labeled a number of specimens in the Lausanne herbarium with both names. Moenkemeyer (1927) stated that *Leskea saviana* De Not. is identical with *P. illyrica* Glowacki, and in 1938 Meylan agreed with him.

Pilous in 1955 described and illustrated some new forms of *L. saviana* from Czechoslovakia, but I have not seen his specimens. All species of *Lescuraea* are quite variable, but to name every form does not simplify the situation.

4. *Lescuraea radicosa* (Mitt.) Moenkem. Die Laubm. Eur. 693. 1927.

Hypnum tenax sensu Drummond, Musci Am. 225 in part. 1828 (non Hedw.); Drummond in Hooker, Bot. Misc. 1: 204. 1830 (nomen nudum).

Hypnum congestum Wils. Ms. (nomen nudum).

Pseudoleskea congesta B.S.G. Bryol. Eur. fasc. 49–51. 1852 (nomen nudum).

Hypnum radicosum Mitt. Jour. Linn. Soc. Bot. 8: 31–32. 1865.

Macounia sciuroides Kindb. Enum. Bryin. Exot. 24. 1888 (nomen nudum).

Pseudoleskea sciuroides Kindb. in Macoun, Bull. Torrey Club 17: 276. 1890.

Pseudoleskea radicosa Kindb. in Macoun, Cat. Can. Pl. 6: 181. 1892.

Ptychodium Pfundtneri Limpr. Die Laubm. 2: 796–799. 1895.

Pseudoleskea bicolor Kindb. Eur. & N. Am. Bryin. 53. 1896.

Pseudoleskea rigescens var. Howei Best, Bull. Torrey Club 27: 233. 1900.

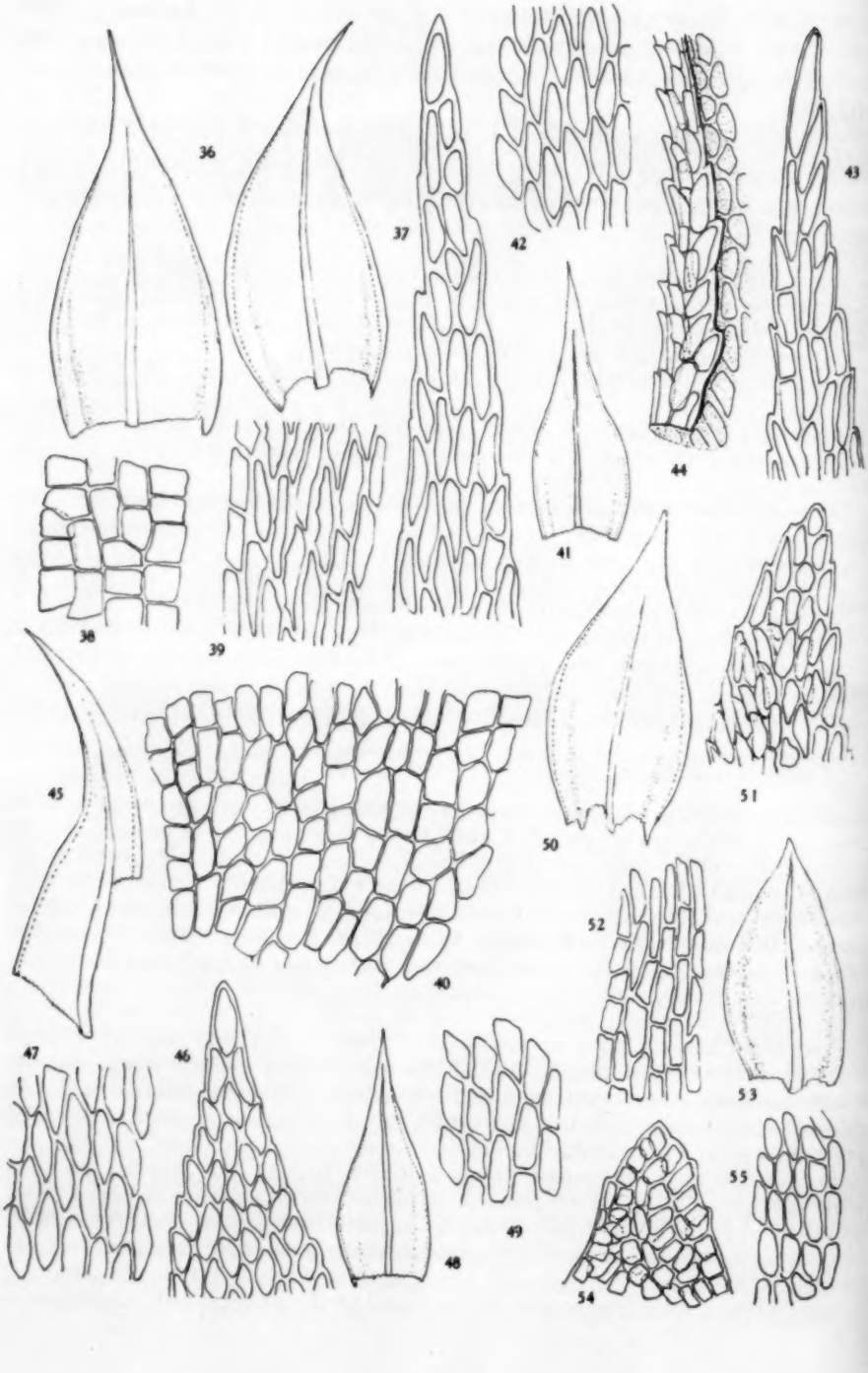
Lescuraea radicosa var. *Pfundtneri* Moenkem. Die Laubm. Eur. 693. 1927.

Pseudoleskea radicosa f. *tenella* Meylan, Revue Bryol. Lichénol. 9: 136–138. 1936.

Pseudoleskea howei Koch, Revue Bryol. Lichénol. 24: 224. 1955.

Plants growing in mats sometimes interwoven but frequently with many long stems nearly parallel, dark green to yellow green or tinged with brown when old; stems prostrate, usually long; branches irregularly arranged, usually hooked at tips; rhizoids in tufts, usually common on both stems and branches, but branches and rhizoids few or none in one variety; paraphyllia numerous and similar to those of *L. patens*. Stem leaves falcate and asymmetric with ovate base and acute apex or long acuminate, the acumen usually shorter than or equal to body of leaf, plicate, decurrent, 1.2–2.4 × 0.25–1.0 mm.; margin entire or more often toothed at apex, recurved from base to apex or recurved at base of leaf and base of acumen with part of margin plane; midrib strong, ending before apex, usually rough on back near apex; alar cells quadrate; median cells of well developed stem leaves variable, mostly 25–45 × 8–10 μ, but shorter cells often present; apical cells similar to median or shorter; cells clear, not opaque, walls not strongly thickened. Branch leaves similar but smaller, usually with shorter cells, more frequently papillose. Cells smooth or more often papillose especially at tips of young branch leaves; papillae formed by projecting cell ends, present on upper surface and back of midrib, rarely on back of lamina.

Sex organs and bracts similar to those of *L. patens*, but the capsules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often larger; capsules usually curved and asymmetric but occasionally erect ones are found; peristome and spores as for *L. patens*, or peristome with well developed cilia.

This is the commonest, most widespread and most variable species consisting of four fairly distinct varieties with some intergrading forms which may be distinguished by the following key:

1. Branches and rhizoids commonly present, usually numerous; leaves often papillose.
   2. Stem leaves long acuminate with apical cells mostly 30 μ long or longer.
      3. Stem leaves 0.3 mm. wide or less ..... 4 a. var. *radicosa* f. *jemtlandica*.
      3. Stem leaves more than 0.3 mm. wide.
         4. Stem leaves 1.2–1.6 × 0.35–0.6 mm. ..... 4 a. var. *radicosa* f. *radicosa*.
         4. Stem leaves mostly 1.6–1.8 × 0.6–0.8 mm. ..... 4 a. var. *radicosa* f. *bernardensis*.
         4. Stem leaves variable reaching 1.7–2.0 × 0.65–0.8 mm. on a part of the plant but with many leaves 1.6 × 0.6 mm. or less ..... 4 a. var. *radicosa* f. *holzingeri*.
   2. Stem leaves acute or with short acumen; apical cells short, less than 30 μ long.
      5. Branch leaves strongly concave at apex; leaves a clear light green ..... 4 d. var. *pallida*.
      5. Branch leaves not strongly concave at apex; leaves green to brownish ..... 4 c. var. *compacta*.
1. Branches and rhizoids few or none; papillae rare; stem leaves 1.7–2.4 μ × 0.7–1.0 mm. ..... 4 b. var. *denudata*.

4 a. *Lescuraea radicosa* var. *radicosa*.

Stem leaves commonly 1.2–1.6 × 0.25–0.6 mm., but reaching 2 × 0.8 mm. in large forms, acumen long, one third to half the leaf length, rarely longer; median cells mostly 25–40 μ long, but some shorter cells often present; apical cells mostly similar to median. Branch leaves usually papillose at tips on upper side and on back of midrib, rarely on both sides of lamina, occasionally smooth.

In forma *radicosa* the stem leaves are 1.2–1.6 × 0.35–0.6 mm., rarely to 0.65 mm. wide (figs. 36–44).

Type: British Columbia, Drummond, Musci Am. 225 in part (holotype NY!).

Common on rocks, rarely on the ground. Found in mountainous regions of Alaska, British Columbia, Alberta, Washington, Oregon, California, Montana, Idaho, Nevada, Utah, Wyoming, Colorado, Arizona; rare east of Rocky Mountains but found in northern Michigan, New Hampshire,

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FIGS. 36–44. *L. radicosa* var. *radicosa*, Drummond, Musci Am. 225, type. FIG. 36. Stem leaves. × 38. FIGS. 37, 38 and 39. Apical, alar and median cells of stem leaf. × 360. FIG. 40. Basal cells of stem leaf from midrib at right to fold at left. × 360. FIG. 41. Branch leaf. × 38. FIGS. 42 and 43. Median and apical cells of branch leaf. × 360. FIG. 44. Cells near apex of branch leaf showing papillae on revolute margin. × 360.

FIGS. 45–49. *L. radicosa* var. *compacta*, Macoun, 1890, type. FIG. 45. Stem leaf. × 38. FIG. 46 and 47. Apical and median cells of stem leaf. × 360. FIG. 48. Branch leaf. × 38. FIG. 49. Median cells of branch leaf. × 360.

FIGS. 50–55. *L. radicosa* var. *pallida*, Brandegee s.n., type. FIG. 50. Stem leaf. × 38. FIGS. 51 and 52. Apical and median cells of stem leaf. × 360. FIG. 53. Branch leaf. × 38. FIGS. 54 and 55. Apical and median cells of branch leaf. × 360.

Labrador, Gaspé Peninsula; in Norway, Sweden and throughout the mountains of southern Europe.

Illustrations:—Limpr. (1895) f. 348; Best (1900) pl. 8, f. 1–9, 30, 31; Sharp (1934) pl. 54, f. 1–9, 30, 31.

Representative specimens examined:—Alaska: Glacier Bay, Trelease and Saunders, June 11, 1899, Harriman Exp. 1911 (MO); Whittier west of Passage Canal, Harvill 518 (CAN); Muir Glacier, J. Cripe, June 10, 1911 (S–PA). British Columbia: near Portage River about Latitude 52° N., Longitude 118° W., Drummond Musci Am. 225 in part (holotype NY); Rocky Mts., Elk River, Dawson, 1883, type of *P. sciuroides* (S–PA); Bear Lake near Sandon, McFadden, May 13, 1926 (NY, MICH, IA); Lake Lindeman, Upper Yukon District, Williams 656 (NY, US). Alberta: Waterton Lakes Park, Cameron Lake, Crum & Schofield 5678; Brewster Creek west of Banff, Crum & Schofield 3123 (CAN); Jasper Park, Wilcox Pass, Lawton 1415 (LAWTON). Washington: Cascade Mts., Goat Mts., Allen, Mosses of Cascade Mts. 96 (NY, US, DUKE, IA, WTU). Oregon: Baker Co., Cornucopia, Frye, June 30, 1935 (WTU, IA, LAWTON); Umatilla Co., Frazier Creek south of Frazier Ranger Station, Weber 2946 (COLO, IA). California: Modoc Co., Big Valley Mts., Baker & Nutting, June 15, 1894 (NY); Siskiyou Co., Sisson southern Trail on Mt. Shasta, Cooke 14652, 14654, 15616a (NY, MICH); Sierra Co., seven miles east of Yuba Pass, route 49, Lawton 3131 (WTU, LAWTON). Montana: Park Co., Gallatin Forest, Camp Joseph, Lawton 2126 (US, DUKE, CAN, LAWTON); Flathead Co., Columbia Falls, Williams 364 (NY, WTU). Idaho: Traille River Basin, Sept. 1889, Leiberg 220 (NY, US, MICH, CAN, S–PA); Kootenai Co., Hope, Sandberg, McDougall & Heller 1171 (NY, US, CAN); Adams Co., Bear, Stanford 1843 (WTU, DUKE, IA, CAN). Nevada: White Pine Co., Snake Mts., Baker Creek, Lawton 2814 (WTU, LAWTON); Ormsby Co., east of Lake Tahoe, Lawton 3101 (WTU, LAWTON). Utah: Salt Lake Co., Wasatch Mts., Little Cottonwood Canyon, Flowers 3428 (UT–F); San Juan Co., La Sal Mts., Flowers 2745 (UT–F). Wyoming: Yellowstone Park, Old Faithful, along Firehole River, Conrad, Sept. 4, 1948 (IA); Park Co., Bear Tooth Lake, Lawton 1943 (LAWTON). Colorado: Gilpin Co., Tolland, Jenny Creek, Grout, N. Am. Musci Pl. 466 (NY, US, MICH, S–PA); Gunnison Co., northwest of Schofield Pass, Weber 9223 (COLO, LAWTON). Arizona: Coconino Co., Aubineau Spring Meadow, San Francisco Peak, Haring 11834 (ARIZ.). Michigan: Keweenaw Co., Copper Harbor, Steere, July 1933 (NY, MICH). Labrador: Battle Harbor, Waghorne, 1891 (NY, US). Newfoundland: White Bay, Waghorne, 1891 (CAN). Quebec: Gaspé Peninsula, Mt. Albert, Allen, July 23, 1881 (NY, US). New Hampshire: White Mts., Tuckerman Ravine, Allen 1880 issued by Grout, N. Am. Musci Pl. 399 (NY, CAN), Faxon, July 18, 1884 (NY). Norway: Seljestad, Nicholson & Dixon, July 21, 1900 (NY). Sweden: Lapponia Tornensis, Jebrenjokk, Jäderholm, July 18, 1912 (NY, S–PA); Patsovara, Jäderholm, Aug. 9, 1917 (S–PA). Austria: Otztaler Alps, am Rettenbach-Ferner, Bergner, July 1932 (S–PA). Switzerland: Simplon, Chambezy 190 from herb. Schleicher (IA). France: Forêt d'Arc sur Lanslebourg, Allorge, 1920 (PG). Italy: Prov. Como, Monte Leguine, Artaria, Sept. 16, 1896 (CAN).

In 1896 Kindberg named a plant *Pseudoleskea bicolor*, but a study of the type collected by Nyman in 1893 in Sweden, Lapponia Luluensis,

Kvikkjokk from the Kindberg herbarium (S–PA) shows that it is variety *radicosa*, similar to the typical form in structure and differs only in color. In this specimen the lower leaves are reddish-brown and the leaves at the tip of the stem are yellow brown, a condition not uncommon in plants in the far north.

The type of Best's *P. rigescens* var. *Howei* collected by M. A. Howe, Aug. 5, 1894 in California on rock near Mt. Shasta was studied (NY) and it is clearly *L. radicosa* var. *radicosa*. The differences between *L. radicosa* and *L. stenophylla* are summarized under *L. stenophylla*.

The plant described by Meylan in 1936 as *P. radicosa* forma *tenella* is forma *radicosa*; in 1938 Meylan concluded that his specimen was *P. stenophylla*, but an examination of his type material (LAU) which was collected on quartzite in 1934 in Switzerland, Col des Essets, Alpes Vaudoises, shows that it is not *L. stenophylla*. The structure of the papillae and the habitat are the best means of distinguishing these plants when sterile. *L. radicosa* grows on rock while *L. stenophylla* is found on wood, generally on the branches of living trees.

4 a. **Lescuraea radicosa** var. **radicosa** f. **jemtlandica** (Kindb.) comb. nov.

Pseudoleskea jemtlandica Kindb. Skand. Bladmfl. 27. 1903.

Pseudoleskea radicosa var. *jemtlandica* Hagen, Kgl. Norske Vidensk. Selsk. Skr. 1908(9): 65. 1909.

Pseudoleskea radicosa var. *radicosa* f. *jemtlandica* Jens. Skand. Bladmfl. 1939 (original not seen).

This is a slender plant with leaves gradually long acuminate; leaves narrow under 0.3 mm. wide. The leaves resemble those of *L. stenophylla* in shape but the papillae are similar to those of *L. radicosa* and on the authority of Hagen (1909) the capsules are typical of *L. radicosa*.

Type: Sweden, Jämtland, Stenfjallet near Storlien. A specimen from the type locality, collected by Adlers Aug. 9, 1882 was loaned by Riksmuseum, Stockholm for study.

4 a. **Lescuraea radicosa** var. **radicosa** f. **bernardensis** (Amann) comb. nov.

Pseudoleskea radicosa var. *bernardensis* Amann, Flore Mousses Suisse 3: 127–128. 1933.

This is a large form of variety *radicosa* and differs in no important character except size; stem leaves mostly 1.6–1.8 × 0.6–0.75 mm.; branch leaves papillose and serrulate at apex.

Type: Switzerland, Amann s.n. (holotype LAU!).

Found in the mountains of southern Europe and rarely in America in situations which are generally moister than for the typical form.

Specimens examined:—Switzerland: Valais, Grand St. Bernard,

Amann, Sept. 21, 1920 (holotype LAU); Brienserroshorn, Amann & Meylan, July 1911 (LAU). Germany: Jaeger Herbarium 155G (NY).

Amann described his variety *bernardensis* as without papillae, paraphyllia few and stem leaves scarcely plicate; but the type specimen shows papillae on the branch leaves and paraphyllia quite common on the stems. In 1938 Meylan came to the conclusion that variety *bernardensis* was identical with *Pseudoleskea denudata* variety *holzingeri* of Best, and thus he placed variety *holzingeri* under *P. radicosa*. There is no doubt but that Meylan is correct in relating his variety *bernardensis* to *L. radicosa*, for a study of the type and of a number of other specimens of his variety from the mountains of southern Europe which were loaned by the Lausanne herbarium shows clearly that Amann's variety differs in no way from *L. radicosa* var.*radicosa* except in size. The fundamental cell structure of the stem leaves is precisely that of typical *L. radicosa*.

4 a. **Lescuraea radicosa** var. **radicosa** f. **holzingeri** (Best) comb. nov.
Pseudoleskea denudata var. *Holzingeri* Best, Bull. Torrey Club 27: 229–230. 1900.

Plants usually with many branches, rhizoids common; some stems of a plant with leaves 1.6–2.0 × 0.6–0.8 mm., without papillae; the same plant with many stems or branches with leaves 1.6 × 0.6 mm. or smaller, papillae present at tips. Peristome with well developed cilia in some specimens.

Type: Montana, Holzinger and Blake s.n. (holotype NY!).

Found in British Columbia, Washington, Montana.

Illustrations:—Best (1900) pl. 8, f. 28, 29; Sharp (1934) p. 53, f. 28, 29.

Specimens examined:—British Columbia: Jackson Basin, Sandon, on rock, McFadden, June 26, 1926 (NY, IA, MICH); Sandon above Rampler Mine, McFadden, Sept. 10, 1927 issued by Bauer, Musc. Eur. et Am. 2181 (NY). Washington: Cascade Mts., Goat Mts., Allen, Mosses of Cascade Mts. 95 (NY, MICH, DUKE, US). Montana: Flathead Co., near Lake McDonald, 4 mi. north of Belton and 30 mi. east of Kalispell, Holzinger & Blake, July 14–30, 1898 (type in Best herbarium NY); Flathead Co., Columbia Falls, Williams 343 (NY).

This form is not uncommon in the western part of North America, but in Europe its place seems to be taken by the form *bernardensis*. It is close to form *bernardensis* but is usually a lighter green in color and with clearer cells and is less uniform as to leaf size. It is intermediate between typical *radicosa* and var. *denudata*, and it differs from variety *denudata* in bearing many branches and rhizoids and in having many relatively small leaves similar to those of form *radicosa*. But on the same plants there are large leaves which cannot be distinguished from those of variety *denudata*.

4 b. **Lescuraea radicosa** var. **denudada** (Kindb.) comb. nov.
Pseudoleskea sciuroides var. *denudata* Kindb. in Macoun, Cat. Can. Pl. 6: 181. 1892.
Ptychodium hyperboreum C. Müll. in litt. 1892.
Ptychodium oligocladum Limpr. Die Laubm. 2: 801. 1895.
Pseudoleskea hyperborea Kindb Eur. & N. Am. Bryin. 52. 1896.

Pseudoleskea sciuroides subsp. *denudata* Kindb. Can. Record of Sci. 6: 20. 1894 (nomen nudum); Kindb. Eur. & N. Am. Bryin. 52. 1896.

Pseudoleskea Breidleri Kindb. Eur. & N. Am. Bryin. 54. 1896.

Pseudoleskea denudata Best, Bull. Torrey Club 27: 229. 1900.

Lescuraea breidleri Arn & Jens. Naturwiss. Untersuch. Sarekgeb. Schwed.-Lappl. 3: 212. 1910.

Lescuraea denudata Moenkem. Die Laubm. Eur. 693–694. 1927.

Lescuraea denudata var. *hyperborea* Moenkem. Die Laubm. Eur. 694. 1927.

Plants growing in loosely spreading mats, usually pale green to whitish; stems 5–10 cm. long, hooked at ends, without branches or with very few branches; usually without rhizoids, paraphyllia numerous and large. Lower stem leaves often broken, the upper falcate, asymmetric, with a broad base and either a long acuminate apex or a short acumen, concave, strongly plicate, decurrent, 1.7–2.4 × 0.7–1.0 mm.; margins recurved nearly to apex, entire or rarely very slightly serrulate at leaf tips; midrib strong, ending below apex; alar cells quadrate; median cells sublinear, mostly 30–45 × 6–8 μ; basal cells commonly shorter and broader than median; cells clear and usually without papillae in upper part of leaf but often weakly papillose on basal recurved margin by the thickened walls of adjacent cells.

Antheridia and perigonial bracts similar to those of *L. patens*; perichaetial bracts to 2.5 mm. long, abruptly acuminate. Seta about 15 mm. long; capsule reddish brown, curved and asymmetric; urn 2–2.5 mm. long; operculum conic; outer peristome to 0.6 mm. long with prominent lamellae and fine horizontal lines except at apex, teeth united at base to form a dark band 5 or 6 joints high; endostome yellowish, basal membrane nearly half its length; segments about as long as teeth, keeled and open on keel; cilia rudimentary, spores papillose, 16–18 μ (figs. 56–59).

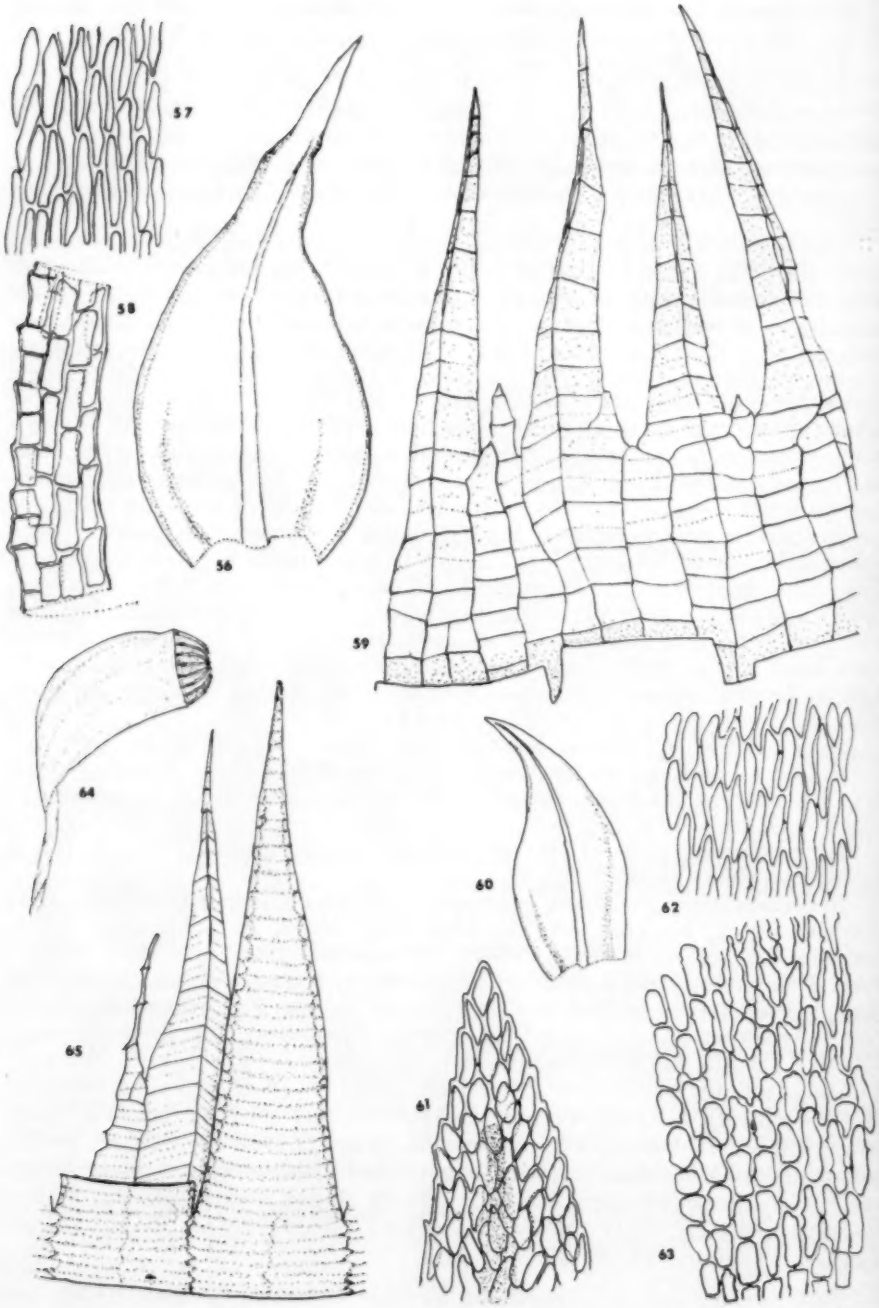
Type: British Columbia, Macoun, Can. Musci 564 (holotype S–PA!).

Found on soil and rotten wood, rarely on stones, from British Columbia, Washington, Montana, Iceland, Norway, Sweden and the mountains of southern Europe.

Illustrations:—Best (1900) pl. 7, f. 22–27; Moenkem. (1927) f. 155 g, h; Sharp (1934) pl. 53, f. 22–27.

Representative specimens examined:—British Columbia: Selkirk Mts., Asulcan Creek, Macoun, Aug. 7, 1890, Can. Musci 564 (holotype S–PA, isotypes US, NY); Asulcan Valley, Brinkman, 1908 (S–PA); Roger's Pass, Brinkman, June 3, 1908 (US); Wilmer, Paradise Mine, McFadden, Aug. 1, 1928, issued by Bauer, Musci Eur. et N. Am. 2182 as var. *holzingeri* (NY). Washington: Jefferson Co., Olympic Peninsula, Hoh River, Becking 5309977 (WTU, LAWTON). Iceland: Dr. Meyer, 1931 (LAU). Norway: Tromsoe, montis Flöjfjellet, Zetterstedt, Aug. 19, 1868 (S–PA); Nordcap, W. Bauer, July 29, 1892, type of *P. hyperboreum* (S–PA). Sweden: Lapponia Tornensis, Vassitjakko, Jäderholm, Aug. 2, 1916 (S–PA, NY). The following are somewhat smaller than typical specimens but resemble the variety in other characters: Hungary: Tatra Magna near lacum Batizovske, Podpěra, July 25, 1921 (S–PA). Austria: Balanspike bei Zederhaus im Jungau, Breidler, Oct. 24, 1885 (LAU).

This variety can be recognized by the very large leaves which are smooth or only feebly papillose and by the absence of branches and rhizoids.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The leaves are usually long acuminate, but some of the smaller specimens have broad leaves with a short acumen. The type material of variety *denudata* was widely distributed and was described as sterile, but the specimen at the United States National Herbarium has a few capsules which are somewhat larger than for variety *radicosa*.

The most significant point which indicates that this plant is a variety and not a species is to be found in the size of the leaves in the form *holzingeri* which has some stems with leaves that are typical of the variety *denudata* while other stems or branches of the same plant bear rather small papillose leaves which cannot be distinguished from the form *radicosa* in any way.

The leaves of variety *denudata* are largest near the tips of the stems with smaller leaves near the base. It seems highly probable that the branches formed in the less favorable part of the growing season may continue to grow under more favorable conditions and produce the large leaves typical of variety *denudata*. Mrs. McFadden collected plants in British Columbia from the same locality in different years and sometimes the specimens were the variety *denudata* and at other times they were the form *holzingeri*. The plant is large and vigorous under good growing conditions and under poor conditions it is smaller and intermediate. It may be that one plant under different condition can produce form *radicosa*, form *holzingeri* and variety *denudata*.

The specimens of Grout's N. Am. Musc. Pl. 455 at the New York Botanical Garden issued as *P. denudata* are *L. radicosa* of the typical form.

4 c. **Lescuraea radicosa** var. **compacta** (Best) comb. nov.

Pseudoleskea radicosa var. *compacta* Best, Bull. Torrey Club 27: 231. 1900.

Plants dark green or brownish to blackish, with short stems and many short branches or with stems and branches rather well developed but never as long as in variety *radicosa*; stems often defoliate with only branch leaves present. Stem leaves similar to those of variety *radicosa* but usually smaller and with a shorter acumen; median cells often shorter than in the typical variety, apical cells less than 30 μ long. Branch leaves smaller, cells shorter (figs. 45–49).

Type: British Columbia, Macoun, July 31, 1890 (holotype NY!).

Not uncommon in western parts of North America where the typical variety is found, also in Europe.

Specimens examined:—British Columbia: Selkirk Mts., Roger's Pass, Macoun, July 31, 1890 (NY); Wilmer, Paradise Mine, McFadden 1107, in Bauer's Musc. Eur, et Am. 2183 as *P. pallida* (NY, IA); London, Jackson

FIGS. 56–59. *L. radicosa* var. *denudata*, Macoun, Can. Musci 564, type. FIG. 56. Stem leaf ×38. FIG. 57. Median cells of stem leaf. ×360. FIG. 58. Cells on recurved margin near base. ×360. FIG. 59. Part of inner peristome from isotype. ×175.

FIG. 60–65. *Lescuraea atricha*. FIGS. 60–63, Macoun s.n. type. FIG. 60. Stem leaf. ×38. FIGS. 61 and 62. Apical and median cells of stem leaf. ×360. FIG. 63. Basal cells of stem leaf from midrib at right to fold at left. ×360. FIG. 64 and 65, Frye 546. FIG. 64. Capsule. ×14. FIG. 65. Part of peristome. ×175.

Basin, McFadden 282, June 26, 1926 (NY). Alberta: Waterton Lakes Park, trail around Bertha Lake, Crum & Schofield 5991 (CAN). Montana: Glacier National Park, Mineral Park, M. E. Jones 10990, Aug. 8, 1910 (NY, IA, LAWTON). Wyoming: Teton National Park, trail to Taggart Lake, Lawton 1744 (LAWTON). Utah: San Juan Co., La Sal Mts., Geyser Pass, Flowers 2829 (UT–F). Colorado: Brandegee, 1877, det. as *H. atrovirens* var. *brachyclados* (NY). Arizona: Coconimo Co., Aubineau Spring Meadow, San Francisco Peak, Haring 11834 (ARIZ, LAWTON). Labrador: Cape Charles, Waghorne, Sept. 12, 1893 (NY). Sweden: Lapponia Tornensis, Vilkisorta, Jäderholm, July 15, 1915 (NY).

This variety differs from variety *radicosa* in the shorter acumen of the leaves and shorter apical cells, from variety *pallida* in the darker color and in having leaves less concave near the apex. It is frequently confused with *L. incurvata* but it can be distinguished by the cells more uniform in size and shape, more angular and with thinner walls, and in general a clearer less opaque appearance.

4 d. **Lescuraea radicosa** var. **pallida** (Best) comb. nov.

Pseudoleskea pallida Best, Bull. Torrey Club 27: 227–228. 1900.

Plants smaller than in variety *radicosa*, in many cases apparently composed entirely of branches with the stems defoliate or nearly so; paraphyllia abundant at least on stems and large branches; branches often scarcely curved at tips. Stem leaves when available with many median cells 25–30 μ long. Branch leaves strongly concave especially at the acute apex, clear light green, composed of thin walled cells which are relatively short with many under 25 μ in length. Papillae and reproductive structures as for the species (figs. 50–55).

Type: Colorado, Brandegee s.n. (holotype NY!).

In mountainous regions at high altitudes, usually near regions of melting snow, and apparently a plant of a short growing season. Found in Colorado, Wyoming, Montana, Utah, Idaho.

Illustrations:—Best (1900) pl. 7, f. 16–21; Sharp (1934) pl. 53, f. 16–20.

Specimens examined:—Colorado: within 100 miles of Canyon City, Brandegee, 1874–1878 (holotype NY). Montana: Sweetgrass Co., Crazy Mts., Iltis 4626 (UARK, LAWTON); Carbon Co., Rock Creek, just north of Montana-Wyoming line, Lawton 2145 (LAWTON). Wyoming: Carbon Co., Medicine Bow Mts., 2.3 miles west of French Creek, Lawton 1697 (LAWTON). Idaho: Custer Co., Adair Creek, Lucky Boy Mine, McFadden 17815, Aug. 7, 1941 (DUKE, CAN). Utah: San Juan Co., La Sal Mts., near Geyser Pass, Flowers 2746 (UT–F).

In 1955 Pilous named a number of forms and a new variety, *balanica* under *L. radicosa*, but I have not seen his specimens. From his excellent illustrations it is clear that similar forms are common throughout the range of the species, but it is doubtful that a multiplication of names is helpful.

5. **Lescuraea atricha** (Kindb.) comb. nov.

Pseudoleskea atrovirens var. *atricha* Kindb. in Macoun, Cat. Can. Pl. 6: 180. 1892.

Pseudoleskea atricha Kindb. Ottawa Nat. 7: 20. 1893.

Plants in mats, yellow green or brownish; stems prostrate, branches numerous, often green at tips, either hooked or nearly straight; rhizoids in

tufts, numerous on specimens growing on wood, but less common on rock inhabiting plants; paraphyllia lanceolate to linear, sometimes few on branches but common on stems. Stem leaves with ovate base, either abruptly short acuminate or gradually long acuminate, falcate and asymmetric or straight and symmetric, plicate, decurrent, 0.8–1.4 × 0.3–0.55 mm., but commonly 1.2 × 0.4 mm.; margin usually serrulate at apex, recurved nearly to apex or part of margin plane; midrib strong, subpercurrent; alar cells mostly quadrate; median cells long and narrow, about 25–35 × 7 μ, rarely to 40 μ long; basal cells 8–10 μ wide and 2 or rarely 3 times as long; cells mostly with thick pitted walls, the pits especially prominent at leaf base. Branch leaves similar but smaller and walls less pitted, more strongly papillose. Papillae on back of midrib and on both sides of lamina, formed by projecting ends of cell walls.

Antheridia and bracts similar to those of *L. patens* except that cell walls of bracts may be pitted; perichaetial bracts abruptly acuminate, midrib weak, cell walls pitted. Seta about 1 cm. long; capsule inclined to horizontal, asymmetric, urn about 1.6 × 0.9 mm., reddish brown; calyptra and operculum not seen; teeth of outer peristome united for about four joints and similar to those of *L. patens;* inner peristome with basal membrane about one third its length; segments nearly as long as teeth, keeled, open on keel; cilia rudimentary; spores 10–15 μ (figs. 60–65).

Type: British Columbia, Macoun s.n. (holotype S–PA!).

Usually on rock, rarely on wood. Alaska, British Columbia and Washington.

Specimens examined:—Alaska: Whittier, Lat. 60° 46′ N., Long. 148° 41′ W., on ledge of mountain, Harvill 941a, 956a, reported as *P. atrovirens* (MICH). British Columbia: Gold Range north of Griffin Lake, on rock, Macoun, Aug. 13, 1889 (holotype S–PA, isotypes NY, US). Washington: Jefferson Co., Olympic Mts., Elwha River Valley on rock, Frye 546 (WTU, NY, CAN, LAWTON); Pierce Co., Mt. Rainier, C. V. Piper 234, Aug. 1895 (NY); Mt. Rainier, south of McClure Cliff, base of Alaska cedar, A. S. Foster 1020, Aug. 5, 1909, issued by Grout, N. Am. Musc. Pl. 336 (NY, WTU, S–PA, CAN, US); Mt. Rainier, J. M. Grant 356, Aug. 1925, det. as *P. substriata* (NY, WTU); Mt. Rainier, near Tipsoo Lake along trail from Tipsoo Lake to Dewey Lake, on rock, Lawton 3506 (WTU, LAWTON).

This species can be distinguished by the thick-walled cells which are plainly pitted in the stem leaves and by the papillae which are usually present on both sides of the lamina at tips of young leaves. *L. saviana* also has papillae on both sides but the leaves are more strongly asymmetric and more conspicuously revolute on the acumen, the cell walls are thinner and pits are not common. *L. stenophylla* is frequently papillose on both sides of the lamina, but the papillae are on the lumen at the end of the cell and the walls are not usually pitted.

The specimens reported from Alaska by Stair (1947) are not this species but *L. stenophylla*. *L. atricha* is rather rare with only seven collections known to the author, one with capsules, Frye 546.

(To be continued)

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TORREYA

Benjamin Minge Duggar

The death of Benjamin Minge Duggar in New Haven, Connecticut on September 10, 1956 at the age of 84 brought to a close the brilliant career of one of the real pathfinders of American science. For here was a man who in his early years had helped lay the very foundations upon which the phytopathological branch of plant science in this country was to be built; and yet, nearly half a century later, this same man, still alert, insatiably curious and critically observant, was to achieve world renown in an entirely different field as discoverer of the antibiotic Aureomycin.

Dr. Duggar was born at Gallion, Alabama on September 1, 1872, the son of a physician, Reuben Henry Duggar, and Margaret Louisa (Minge) Duggar. He attended

Benjamin Minge Duggar September 1, 1872–September 10, 1956.

private schools and studied with tutors prior to beginning his formal education in 1887 at the University of Alabama where he remained for two years. His father's horticultural and gardening activities had kindled in the youthful Duggar a keen interest in plants and their behavior. These feelings were intensified as a result of contacts with a druggist friend of his father who possessed an outstanding collection of native American botanical specimens. Because of greater opportunity to develop this growing interest in biological sciences, he transferred to Mississippi State College where, in

1891, he was awarded a B.S. degree with highest honors. His subsequent association with Professor George F. Atkinson at the Alabama Polytechnic Institute, where in 1892 he received the M.S. degree, marked the beginning of what was to be a lifelong devotion to the study of fungi.

As recipient of a scholarship, Dr. Duggar entered Harvard in the fall of 1893, there earning a B.A. degree in 1894 and a year later the M.S. degree. After working with the Illinois State Natural History Laboratory for a year, he accepted the invitation of his old friend Professor Atkinson, now at Cornell University, to join him there as instructor in Botany. This position afforded him an opportunty to continue his graduate study on plant diseases and in 1898 he was awarded the Ph.D. degree. In a move characteristic of his vigorous pursuit of knowledge, Dr. Duggar spent the next 18 months in Europe studying in the laboratories of Wilhelm Pfeffer at Leipzig and Georg Klebs at Halle.

Returning briefly to Cornell University in the fall of 1900, this time as assistant professor, Dr. Duggar was soon called to the Bureau of Plant Industry of the United States Department of Agriculture. In this position he conducted far-reaching investigations relevant to mushroom culture, experimental work which was to result ultimately in the establishment of techniques and practices essential to the sound development of mushroom-growing as an industry in this country. A second U.S.D.A. assignment took him to Texas to study the destructive *Phymatotrichum* root-rot disease of cotton.

In 1902 Dr. Duggar was appointed Professor and Head of the Department of Botany at the University of Missouri, a position he occupied continuously until 1907, with the exception of a year (1905–1906) again spent in European study—this time with Goebel at Munich and with Flahault at Montpellier. Returning once again to Cornell University, now as Professor of Plant Physiology, he turned his attention to scientific writing. His book, "Fungous Diseases of Plants," published in 1909, was the first text on this subject to be written in English and was enthusiastically received by phytopathologists everywhere.

During the next thirty-one years Dr. Duggar's academic career moved to its zenith, first as Research Professor of Plant Physiology at Washington University and the Missouri Botanical Garden (1912–1927) and finally as Professor of Botany and Plant Pathology at the University of Wisconsin (1927–1943). The great number of Duggar-trained men who today occupy responsible scientific positions in many parts of the world are living testimony to his brilliance as a teacher. His tireless research effort during these years brought forth a steady flow of more than one hundred contributions to the published volumes of the many societies with which he was affiliated. So numerous were his honors and official positions in these organizations that we can make no individual note of them here. Representative of some of his activities were leadership in the organization of an International Plant Congress (1926), chairmanship of the National Research Council Committee on the Effects of Radiation on Organisms (1935–1940)—an assignment which included editing the two volume work on "Biological Effects of Radiation", a long term as an editor for Botanical and Biological Abstracts (1917–1933), and election to and active participation in the functions of the National Academy of Sciences and the American Philosophical Society.

In 1943, past the retirement age specified by Wisconsin State law, Dr. Duggar was appointed Emeritus Professor. At this point an honorable finis to a long and distinguished career might well have been written. But, in keeping with his philosophy that physical and mental activity is essential to well-being, Dr. Duggar wasn't ready to retire. He was, therefore, happy to accept in 1944 the invitation of the late Dr. Y. SubbaRow to join the research staff of the Lederle Laboratories Division of the American Cyanamid Co. at Pearl River, New York. Here he spent the remaining twelve years of his life, years devoted to the search for new and better antibiotics. His efforts were rewarded by the isolation of a previously undescribed organism which he named *Streptomyces aureofaciens* and the discovery of its capacity to produce the broad-spectrum antibacterial antibiotic Aureomycin. This final achievement brought to Dr. Duggar worldwide acclaim and an honorary fellowship in the International College of Surgeons. His post-academic years also brought further recognition in the form of

three other honorary degrees from institutions he had served so well—Doctor of Laws from the University of Missouri and Doctor of Science from Washington University at St. Louis and from the University of Wisconsin.

Dr. Duggar's writings and accomplishments remain as a monument and constant reminder of the magnitude of his professional skill. But to his many associates he was much more than a great scientist. He was a kind and sympathetic friend who, in his warm, sincere way, could always reach their level and supply the inspiration they needed to face the problems that lay ahead. This small, quiet southern gentleman was, indeed, a giant.—EDWARD J. BACKUS, Lederle Laboratories Division, American Cyanamid Company.

An Annotated Preliminary Catalogue of the Vascular Flora of Rockland County, New York

(Continued from Bull. Torrey Club **84**: 206–213, 1957.)

J. HARRY LEHR

ERICACEAE

RHODODENDRON

*RHODODENDRON MAXIMUM L. Rosebay Rhododendron. Haverstraw.
R. NUDIFLORUM (L.) Torr. Pinxter-Flower. General. (H)
R. VISCOSUM (L.) Torr. Swamp-Honeysuckle. Haverstraw, Clarkestown. (H)

KALMIA

*KALMIA ANGUSTIFOLIA L. Sheep-Laurel. Haverstraw. (H)
K. LATIFOLIA L. Mountain-Laurel. General. (H)
K. LATIFOLIA L. forma ALBA (Moullefert) Rehd. General. The variations in color from pink to white are so common in this shrub that it is debatable whether this form is entitled to rank as a taxonomic entity. (H)

LYONIA

LYONIA LIGUSTRINA (L.) DC. Maleberry. Ramapo. (H)

CHAMAEDAPHNE

*CHAMAEDAPHNE CALYCULATA (L.) Moench var. ANGUSTIFOLIA (Ait.) Rehd. Leather-Leaf. Haverstraw. No specimens have been found in the County's mountain bogs. This single station occurs on a pond-margin. (H)

EPIGAEA

EPIGAEA REPENS L. Trailing-Arbutus. Ramapo. (H)

GAULTHERIA

*GAULTHERIA PROCUMBENS L. Wintergreen. Ramapo. (H)

GAYLUSSACIA

GAYLUSSACIA BACCATA (Wang.) K. Koch. Black Huckleberry. General. (H)
*G. FRONDOSA (L.) T. & G. Dangleberry. Ramapo. (H)

VACCINIUM

*VACCINIUM ANGUSTIFOLIUM Ait. var. LAEVIFOLIUM House. Early Low Blueberry. General. (H)
*V. ATROCOCCUM (Gray) Heller. Black Highbush Blueberry. Haverstraw.
V. CORYMBOSUM L. Highbush Blueberry. General. (H)
*V. MACROCARPON Ait. Large Cranberry. Ramapo, Haverstraw. (H)

V. STAMINEUM L. Deerberry. General. (H)
V. VACILLANS Torr. Late Low Blueberry. General.
The author believes he is comparatively "safe" in presenting the preceding species. Further study of the genus may add to the list but should not result in retraction.

PRIMULACEAE

LYSIMACHIA

LYSIMACHIA CILIATA L. Fringed Loosestrife. Ramapo.
L. NUMMULARIA L. Moneywort. Ramapo.
L. QUADRIFOLIA L. Whorled Loosestrife. General. (H)
L. TERRESTRIS (L.) BSP. Swamp-Candles. Ramapo, Haverstraw, Clarkestown. (H)

TRIENTALIS

TRIENTALIS BOREALIS Raf. Star-Flower. Ramapo. (H)

SAMOLUS

SAMOLUS PARVIFLORUS Raf. Water-Pimpernel. Stony Point, Orangetown. (H)

OLEACEAE

FRAXINUS

FRAXINUS AMERICANA L. White Ash. General. (H)
F. NIGRA Marsh. Black Ash. Ramapo. (H)

FORSYTHIA

*FORSYTHIA VIRIDISSIMA Lindl. Forsythia. Remaining after cultivation. Clarkestown, Ramapo. (H)

LIGUSTRUM

*LIGUSTRUM VULGARE L. Privet. Ramapo.

GENTIANACEAE

GENTIANA

*GENTIANA CLAUSA Raf. Bottle-Gentian. There have been previous reports for *G. Andrewsii* from this county but there are no herbarium specimens to substantiate these reports and the author believes the reporters may have been confused in their determinations. Ramapo, Clarkestown. (H)
GICRINITA Froel. Fringed Gentian. Ramapo. (H)

BARTONIA

BARTONIA VIRGINICA (L.) BSP. Yellow Bartonia. Clarkestown, Ramapo. (H)

APOCYNACEAE

VINCA

VINCA MINOR L. Common Periwinkle. Ramapo, Clarkestown. Commonly spread from or remaining after cultivation. (H)

APOCYNUM

APOCYNUM ANDROSAEMIFOLIUM L. Spreading Dogbane. Haverstraw, Clarkestown, Ramapo. (H)
A. CANNABINUM L. Indian Hemp. Ramapo, Clarkestown. (H)
*A. SIBIRICUM Jacq. forma ARENARIUM (F. C. Gates) Fern. Clasping-leaved Dogbane. Haverstraw, Stony Point. (H)

ASCLEPIADACEAE

ASCLEPIAS

*ASCLEPIAS INCARNATA L. Swamp-Milkweed. Ramapo, Clarkestown. (H)
A. INCARNATA L. var. PULCHRA (Ehrh.) Pers. Stony Point. (H)
*A. PURPURASCENS L. Purple Milkweed. Ramapo. (H)
A. QUADRIFOLIA Jacq. Four-leaved Milkweed. Clarkestown. (H)
A. SYRIACA L. Milkweed. General.
*A. SYRIACA L. forma INERMIS Churchill. Orangetown. (H)
A. TUBEROSA L. Butterfly-Weed. Ramapo, Clarkestown. (H)

CYNANCHUM

*CYNANCHUM NIGRUM (L.) Pers. Black Swallow-Wort. Clarkestown. (H)

CONVOLVULACEAE

CONVOLVULUS

CONVOLVULUS ARVENSIS L. Bindweed. Clarkestown, Stony Point. (H)
C. SEPIUM L. Wild Morning-Glory. General. (H)

CUSCUTA

CUSCUTA GRONOVII Willd. Common Dodder. General.

POLEMONIACEAE

PHLOX

PHLOX DIVARICATA L. Blue Phlox. Ramapo, Clarkestown. Locally naturalized; in no instance a native. (H)

P. PANICULATA L. Perennial Phlox. General. A frequent escape and naturalized at a few stations.

P. SUBULATA L. Mountain-Pink. Ramapo. Spread from cultivation rather than naturalized.

BORAGINACEAE

ECHIUM

ECHIUM VULGARE L. Blue Thistle. General. Most frequently found along railroad tracks. (H)

MYOSOTIS

MYOSOTIS LAXA Lehm. Smaller Forget-Me-Not. Clarkestown, Ramapo. (H)
M. SCORPIOIDES L. True Forget-Me-Not. Clarkestown, Ramapo. (H)
M. VERNA Nutt. Early Scorpion-Grass. Clarkestown. (H)

VERBENACEAE

VERBENA

VERBENA HASTATA L. Blue Vervain. General.
V. SIMPLEX Lehm. Narrow-leaved Vervain. Ramapo. (H)
V. URTICIFOLIA L. White Vervain. General. (H)

LABIATAE

TRICHOSTEMA

TRICHOSTEMA DICHOTOMUM L. Blue Curls. General. Most frequently found along railroad tracks. (H)

TEUCRIUM

*TEUCRIUM CANADENSE L. var. VIRGINICUM (L.) Eat. American Germander. Clarkestown. (H)

Scutellaria

Scutellaria epilobiifolia A. Hamilton. Common Skullcap. Stony Point. (H)
S. lateriflora L. Mad-Dog Skullcap. Ramapo, Clarkestown. (H)

Nepeta

Nepeta Cataria L. Catnip. Ramapo.

Glechoma

Glechoma hederacea L. var. micrantha Moricand. Small-flowered Gill-Over-The-Ground. Orangetown. (H)

Prunella

Prunella vulgaris L. Heal-All. General. (H)

Leonurus

Leonurus Cardiaca L. Motherwort. Clarkestown, Ramapo. (H)

Lamium

*Lamium amplexicaule L. Dead Nettle. Ramapo. (H)

Monarda

Monarda didyma L. Oswego-Tea. Ramapo. A single station which the author believes is an escape rather than native. (H)
M. fistulosa L. Wild Bergamot. Ramapo, Haverstraw. (H)

Hedeoma

Hedeoma pulegioides (L.) Pers. American Pennyroyal. Stony Point. (H)

Pycnanthemum

Pycnanthemum incanum (L.) Michx. Hoary Mountain Mint. Stony Point. (H)
P. tenuifolium Schrad. Narrow-leaved Mountain Mint. Clarkestown. (H)
P. virginianum (L.) Durand & Jackson. Virginia Mountain Mint. Ramapo, Clarkestown. (H)

Cunila

Cunila origanoides (L.) Britt. Common Dittany. Clarkestown, Ramapo. (H)

Lycopus

Lycopus americanus Muhl. Cut-leaved Water Hoarhound. Ramapo, Clarkestown. (H)
L. uniflorus Michx. Northern Bugleweed. Ramapo. (H)
L. virginicus L. Bugleweed. Ramapo. (H)

Mentha

M. arvensis L. Wild Mint. Ramapo, Clarkestown. (H)
M. piperita L. Peppermint. Ramapo.
*M. rotundifolia (L.) Huds. Round-leaved Mint. Ramapo.
M. spicata L. Spearmint. Clarkestown, Ramapo. (H)

Collinsonia

Collinsonia canadensis L. Richweed. Ramapo, Clarkestown.

SOLANACEAE

SOLANUM

*SOLANUM AMERICANUM Mill. American Bittersweet. Orangetown.
S. CAROLINENSE L. Horse Nettle. Clarkestown.
S. DULCAMARA L. European Bittersweet. Ramapo. (H)
S. NIGRUM L. Black Nightshade. Ramapo.

DATURA

*DATURA STRAMONIUM L. Jimson Weed. Ramapo. (H)

SCROPHULARIACEAE

VERBASCUM

VERBASCUM BLATTARIA L. Moth Mullein. Ramapo, Clarkestown. (H)
V. THAPSUS L. Mullein. General. (H)

LINARIA

LINARIA CANADENSIS (L.) Dumont. Old-Field Toadflax. Ramapo, Clarkestown. (H)
L. VULGARIS Hill. Butter-and-Eggs. General. (H)

CHAENORRHINUM

*CHAENORRHINUM MINUS (L.) Lange. Small Snapdragon. Clarkestown.

CHELONE

CHELONE GLABRA L. Turtle-Head. General. (H)

PENSTEMON

PENSTEMON DIGITALIS Nutt. Beard-Tongue. Clarkestown, Haverstraw.

PAULOWNIA

*PAULOWNIA TOMENTOSA (Thunb.) Steud. Royal Paulownia. Orangetown. Introduced and naturalized at this its only station. (H)

MIMULUS

MIMULUS RINGENS L. Monkey-Flower. Ramapo, Clarkestown. (H)

LINDERNIA

LINDERNIA DUBIA (L.) Pennell. False Pimpernel. Ramapo, Clarkestown. (H)

VERONICASTRUM

VERONICASTRUM VIRGINICUM (L.) Farw. Culver's-Root. Clarkestown. (H)

VERONICA

VERONICA AMERICANA (Raf.) Schwein. American Brooklime. Clarkestown, Ramapo.
V. ANAGALLIS-AQUATICA L. Water Speedwell. Clarkestown, Ramapo. (H)
V. OFFICINALIS L. Speedwell. General. (H)
V. SCUTELLATA L. Marsh Speedwell. Ramapo, Clarkestown. (H)
V. SERPYLLIFOLIA L. Thyme-leaved Speedwell. Ramapo. (H)

GERARDIA

*GERARDIA FLAVA L. Smooth False Foxglove. Haverstraw. (H)
*G. PEDICULARIS L. Fern-leaved Foxglove. Haverstraw, Ramapo. (H)

G. TENUIFOLIA Vahl. Slender Gerardia. Ramapo, Clarkestown. (H)
G. VIRGINICA (L.) BSP. Downy False Foxglove. Ramapo, Haverstraw. (H)

MELAMPYRUM

MELAMPYRUM LINEARE Desr. var. AMERICANUM (Michx.) Bauverd. Cow-Wheat. Haverstraw, Ramapo, Clarkestown. (H)

PEDICULARIS

PEDICULARIS CANADENSIS L. Lousewort. General. (H)
P. LANCEOLATA Michx. Swamp Lousewort. Clarkestown. (H)

BIGNONIACEAE

CAMPSIS

*CAMPSIS RADICANS (L.) Seem. Trumpet-Flower. Ramapo. Remaining after cultivation. (H)

CATALPA

*CATALPA BIGNONIOIDES Walt. Southern Catalpa. Ramapo. A frequent escape. (H)

OROBANCHACEAE

EPIFAGUS

EPIFAGUS VIRGINIANA (L.) Bart. Beech-Drops. General. (H)

CONOPHOLIS

CONOPHOLIS AMERICANA (L.) Wallr. Cancer-Root. Clarkestown, Ramapo, Orangetown. (H)

OROBANCHE

OROBANCHE UNIFLORA L. One-flowered Cancer-Root. Clarkestown, Ramapo. (H)

PLANTAGINACEAE

PLANTAGO

PLANTAGO LANCEOLATA L. English Plantain. General.
P. MAJOR L. Broad-leaved Plantain. General.
P. RUGELII Dene. Rugel's Plantain. Ramapo.

RUBIACEAE

GALIUM

GALIUM APARINE L. Cleavers. General. (H)
G. ASPRELLUM Michx. Rough Bedstraw. Ramapo.
G. CIRCAEZANS Michx. Wild Licorice. Ramapo, Clarkestown. (H)
G. ERECTUM Huds. Ramapo, Clarkestown.
*G. OBTUSUM Bigel. Stiff Marsh Bedstraw. Ramapo.
G. TINCTORIUM L. Clayton's Bedstraw. Ramapo, Clarkestown.
G. TRIFLORUM Michx. Sweet-scented Bedstraw. Ramapo.
G. VERUM L. Yellow Bedstraw. Clarkestown. (H)

DIODIA

*DIODIA TERES Walt. Buttonweed. A rarity north of New York City. Orangetown. (H)

MITCHELLA

MITCHELLA REPENS L. Patridge-Berry. General. (H)

CEPHALANTHUS

CEPHALANTHUS OCCIDENTALIS L. Buttonbush. General. (H)

HOUSTONIA

HOUSTONIA CAERULEA L. Bluets. Clarkestown. (H)

CAPRIFOLIACEAE

DIERVILLA

DIERVILLA LONICERA Mill. Bush-Honeysuckle. Ramapo, Clarkestown. (H)

LONICERA

*LONICERA DIOICA L. Wild Honeysuckle. Ramapo. (H)
L. JAPONICA Thunb. Japanese Honeysuckle. General.
*L. MAACKII Maxim. Maack's Honeysuckle. Ramapo. An isolated escape on the border of a wooded swamp. Ramapo. (H)
*L. MORROWI Gray. Morrow's Honeysuckle. Ramapo. A single station for this escape. (H)
*L. TATARICA L. Tartarian Honeysuckle. Ramapo. Another escape at a single station. (H)

TRIOSTIUM

TRIOSTIUM AURANTIACUM Bickn. Wild Coffee. Ramapo.

VIBURNUM

VIBURNUM ACERIFOLIUM L. Maple-leaved Viburnum. General. (H)
*V. CASSINOIDES L. Withe-Rod. Clarkestown, Haverstraw. (H)
V. DENTATUM L. Southern Arrow-Wood. Ramapo. (H)
V. LENTAGO L. Nannyberry. Ramapo. (H)
V. PRUNIFOLIUM L. Blackhaw. General. (H)
V. RECOGNITUM Fern. Arrow-Wood. Haverstraw. (H)

SAMBUCUS

SAMBUCUS CANADENSIS L. Common Elder. General. (H)
S. PUBENS Michx. Red-berried Elder. Orangetown, Clarkestown. (H)

VALERIANACEAE

VALERIANA

*VALERIANA OFFICINALIS L. Garden-Heliotrope. An escape at a single station. Clarkestown. (H)

CUCURBITACEAE

ECHINOCYSTIS

*ECHINOCYSTIS LOBATA (Michx.) T. & G. Wild Cucumber. Ramapo, Haverstraw. (H)

CAMPANULACEAE

SPECULARIA

SPECULARIA PERFOLIATA (L.) A. DC. Venus's-Looking-Glass. Ramapo, Clarkestown. (H)

CAMPANULA

CAMPANULA RAPUNCULOIDES L. Bellflower. Clarkestown, Ramapo. (H)
C. ROTUNDIFOLIA L. Bluebell. Stony Point. (H)
C. ROTUNDIFOLIA L. forma ALBIFLORA Rand. & Redf. White Bluebell. Stony Point. (H)

LOBELIA

LOBELIA CARDINALIS L. Cardinal-Flower. Ramapo, Clarkestown, Orangetown. (H)
L. INFLATA L. Indian-Tobacco. General. (H)
L. SIPHILITICA L. Great Lobelia. Clarkestown, Ramapo. (H)
L. SPICATA Lam. Pale-Spike-Lobelia. Ramapo, Clarkestown. (H)

(to be continued)

PROCEEDINGS OF THE CLUB

February 19, 1957. The meeting, at Fordham University, was called to order by President Rickett at 8:00 P.M. There were 57 members and guests present. The minutes of the meeting of February 5 were approved as read. Mr. and Mrs. Aaron Halpern were elected to Associate Membership in the Club. Since there was no further business to be conducted Dr. Rickett introduced the speaker of the evening, Dr. J. Herbert Taylor, of Columbia University who addressed the Club on, "Mode of Replication and Organization of Chromosomes as Revealed by Distribution of Tritium-Labeled DNA". Dr. Taylor's abstract follows:

Thymidine which is a specific and selective label for DNA (deoxyribonucleic acid) was tagged with tritium, the radioactive isotope of hydrogen. When roots were grown in solutions containing the labeled thymidine only the chromosomes in process of duplication were tagged. At the succeeding anaphase the label was distributed equally to each two daughter chromosomes as revealed by autoradiographs. After one replication in the absence of the labeled thymidine, these labeled chromosomes produced one labeled daughter and one completely free of label. Since the new DNA was equally divided, we must assume that the old DNA was also equally divided. However, the new, labeled DNA was built into a unit separate from the old DNA for they separate in an all or nothing fashion at the second division after becoming labeled. We deduce from this behavior that the chromosome is composed of two units or strands, and the suggestion is made that these strands are complementary. The mode of duplication revealed here is analogous to the scheme proposed for the DNA molecule by Watson and Crick.

A certain amount of sister-strand exchange (exchange between daughter chromosomes, but not between the two strands of a single chromosome) occurs between the period of duplication in interphase and the separation of the chromosomes at anaphase. Analysis of the type of rejoining when the exchanges occur indicated that the two strands of a chromosome show opposite parity (or polarity) in reunion. This observation supports the inference that the two units of the chromosome are complementary and therefore each may be capable of acting as a template for the new unit which will be built along it.

After a period of discussion the meeting was adjourned at 9:10 P.M.

Respectfully submitted
Frank G. Lier
Recording Secretary

March 5, 1957. The meeting, at Hunter College, was called to order by President Rickett at 8:00 P.M. Twenty five members and guests were present. The minutes of the previous meeting were accepted as read. Miss Christene Howson was elected to Active (Annual) membership in the Club. Dr. Rickett introduced the speaker of the evening, Dr. Herman F. Becker, of Brooklyn College, who addressed the Club on, "Fossil Plants of Western Montana". Dr. Becker's abstract follows:

A flora from Tertiary shales of the upper Ruby River Basin in southwestern Montana was discussed. Discovery of a widespread paper shale deposit in 1947, and subsequent field work resulted in an extensive accumulation of known and unknown species, second to date only to the classical Florissant flora of Colorado. The Ruby flora yielded 17 species new to science. The method of naming these species was elaborated on as well as the interpretation of this assemblage in regard to scientific value per se, to general environment, ecologic niches, and to climate. Comparison of the Ruby flora with other existing similar floras involves correlation with implications of possible economic

value. Migration of the flora in response to geologic, edaphic, and climatic conditions was traced. Evolution of species, expansion, extinction or retreat to (survival in) Asia follows as a natural conclusion. The sum-total of these factors together with structural and lithologic considerations determined the age of the flora to be late Oligocene.

Historically, credit is given to early (Florissant), later, and modern scientists who, of necessity, specialize in "era" paleobotany. A thorough knowledge of taxonomic rules, leaf form with recognition of the "variation factor" coupled with a fundamental understanding of geologic processes is required. Consulting of previous literature, and an exhaustive comparison of fossil with herbarium material as well as living specimens is imperative to insure a reasonably accurate classification. A comparative study of the living Ruby flora was made. Fossil specimens of leaves and insects were presented and the predominant "*Metasequoia*" character of the flora was established. Photographic plates and drawings of fossil Ruby leaves and flowers and their living analogues were shown. Kodachrome slides showed the fossil localities and the larger physiographic environment of the Ruby Basin.

The talk was followed by a period of discussion and inspection of the exhibits of fossil plants which Dr. Becker had on display.

Tea and refreshments were served by the members of the Hunter College Faculty after the meeting was adjourned at 9:18 P.M.

Respectfully submitted
Frank G. Lier
Recording Secretary

Field Trip Report

April 14. St. John's in the Wilderness. A joint Torrey-Rockland Audubon group attended this service (see Torreya in Bull. Torrey Club 81: 460, 1954, 82: 397, 1955 and 83: 385, 1956). A wooded swamp was explored previous to the service and produced the first report of *Coptis groenlandica* from Rockland County. This plant is a rarity in New York State south of the Hudson Highlands. In addition, the area also contained the largest stand of *Rhododendron maximum* which the leader, a student of the County's flora, has as yet found in the County. The only herbaceous plant found in flower during the day was a single specimen of *Carex pensylvanica*, this notwithstanding the fact that it was the latest Palm Sunday date since the inception of Torrey's participation in this service. Attendance: Torrey 7, Rockland Audubon 7. Leader, J. Harry Lehr.

Book Reviews

Life Forms as Age Indicators. By H. Mølholm Hansen. 48 pp. A. Rasmussens Bogtrykkeri, Ringkjøbing, Denmark, 1956.

The author has set out to answer two questions in this brief but involved monograph: "Does a fossil flora reflect the climatic conditions prevailing when that flora was deposited?" "Can life forms be employed to determine age in botanical systematics?"

An affirmative answer was determined for the first question. This answer is based entirely upon a consideration of the life form spectra of various Quaternary floras and comparisons of Quaternary and modern floras. In concluding this portion of the monograph, the author asserts that, "It is thus beyond doubt that in the life forms we have a means of characterisation of the climatic conditions *of the past.*" In summary of his findings, Dr. Hansen writes, "Biological plant geography has shown that in our time we must take account of four main plant climates: a Phanerophyte climate characteristic of the tropics, a Hemicryptophyte climate embracing the temperate zones of the Earth, a Chamaephyte climate, which occurs where an arctic climate dominates, as well as a Therophyte climate characteristic of the arid zones.

"An examination of the Quaternary floras so far known shows that the biological spectra of these floras comprise the same four main groups, and that each of the four

plant climates deposits floras which are characterised by the life form typical of that part. *A Phanerophyte climate yields a Quaternary flora where the Phanerophytic life form predominates; a Hemicryptophyte climate produces a Quaternary flora where the Hemicryptophytic life form is characteristic; a Chamaephyte climate in the same way deposits a Quaternary flora characterised by Chamaephytes, and a Therophytic climate a Quaternary flora where Therophytes dominate*'' (author's italics).

The contents of 5000 papers, encompassing our present knowledge of the plant life of the Cainophytic period (Cretaceous to Quaternary) were, according to the author, cataloged and used as the *pièce de résistance* for the second answer. Several tables are presented which perplexingly summarize the data for 21,000 species of plants distributed through 3,300 genera. These tables are arranged to illustrate the chronologic sequence of life form development and the climatic patterns of the Cainophytic period.

Interpretation of the data has led the author to conclude that life forms are of different ages. ''The earliest life forms within the flowering plants are the Megaphanerophytes and the Mesophanerophytes, the origin and culmination of which lies in the Cretaceous period. Of later date, belonging to the Palaeogene, are the Microphanerophytes and the Lianas. The next stage in the evolution is represented by the Nanophanerophytes and the Hemicryptophytes, whose development takes place especially in the Neogene. The youngest set of life forms comprises the Chamaephytes and Therophytes, whose development culminates in the Quaternary period. The Geophytes too are comparatively young, and it can be proved by plant geography that they are pre-Quaternary.'' ''Evolution within the Pteridophytes agrees with the Angiospermous groups, the earliest groups of ferns comprising many more Phanerophytic types than the later ones; only the formation of Hemicryptophytes and the rest of the younger life forms started at an earlier period among the Pteridophytes.''

A fundamental aspect of the evolution of life forms has been ''the gradual decline of the height of the species through the ages, from Megaphanerophytes to Mesophanerophytes in the Cretaceous species, through Microphanerophytes in the Palaeogene, Nanophanerophytes in the Neogene to Chamaephytes in the Quaternary species.''

Analyses of the floras of the various geological periods are interpreted by the author to indicate that, ''From a climatic optimum in the Neocomian there occurs in the course of the Cretaceous a slow climatic deterioration which at the beginning of the Tertiary period, probably in the Paleocene, is replaced by another climatic optimum. This climatic optimum is again superseded by a climatic deterioration which continues through the Tertiary period until the Ice Ages of the Quaternary period.'' This paleoclimatic analysis is in accord with the climatic scheme developed from data dealing with terrestrial and marine fossil faunas.

The author summarizes the changes which occurred in the plant world in the course of the Cretaceous by stating that, ''an increasing protection has taken place of the vital organs of the plants against unfavorable external conditions. The carpel closes round the ovule and develops the angiospermous plant, the Cretaceous new formation with the gymnospermous plant of earlier times as its starting point. The perianth . . . closes protectively around the fructification organs and the flowering plant develops, the raments are evolved and close protectively around the vegetative points of the shoots. Towards the close of the period we meet another protective function, the leaf fall. . . .''

This paper is a classic example of circular reasoning: Climate determines life form, life form is a reliable index of climate, the succession of dominant life forms through the various geological periods illustrates the sequence of evolution of the various life forms, and the predominance of a life form in the flora of a given age is an index of the climate of that age.

Throughout the paper there is a suggestion of a mechanistic cause-and-effect relationship and a linear pattern of evolution. For example, on page 34, the author relates that, ''The earliest Cretaceous ice age in the Aptian *resulted* in the appearance of flowering plants'' (italics are the reviewer's).

Dr. Hansen's treatise may prove to be an outstanding theoretical contribution to the field of systematics and paleoecology. Certainly it should stimulate others to attempt to verify his contentions. To fully accept the emphatic statements which Dr.

Hansen has made, however, would require a substantial degree of scientific abandon and an overwhelming faith in the author's interpretation of the unpublished data upon which the conclusions are based. The reader is provided only with well-masticated frass that provides unsatisfactory grounds for personal evaluation of the problems with which the paper is concerned.—JACK MCCORMICK, in charge of Vegetation Studies, The American Museum of Natural History, New York 24, N.Y.

The Study of Plant Communities: an Introduction to Plant Ecology. By Henry J. Oosting. 2nd. ed. W. H. Freeman & Co., San Francisco. 440 pp. 1956.

The second edition of Oosting's "Plant Communities" is an improved version of an already excellent textbook of general plant ecology. The basic organization of the book is unchanged, but several important revisions and additions have been incorporated.

The first chapter is a brief introduction to the field of plant ecology. Chapters two, three, and four describe the nature of plant communities and the methods of vegetational analysis, including some of the plotless methods (pp. 42–43). Environmental factors—climatic, edaphic, and biotic—are treated in chapters five through nine. Chapters ten through twelve deal with community dynamics, and the final chapter takes up the practical or applied aspects of plant ecology.

In the new edition soil is treated more logically in two chapters, one dealing with pedogenesis and the other with edaphology. The chapter on succession and climax has been completely rewritten so as to contrast the elements and applications of both the monoclimax and the polyclimax theories. Many new references have been cited throughout the text in an attempt to keep pace with the rapidly expanding literature.

"Plant Communities" is well suited for its intended purpose—it is an excellent textbook for an introductory course in plant ecology. The organization of the material is logical, the illustrations are well chosen, and the style is clear, concise, and unambiguous. It covers the basic principals of plant ecology very nicely, and it does so briefly without distorting them and without smothering them in a lot of insignificant details. The inclusion of general references at the end of each chapter and of numerous citations in the text provides an excellent point of departure for students interested in further studies.—WILLIAM E. MARTIN, Botany Department, Rutgers, The State University of New Jersey, New Brunswick, N. J.

A Manual of Aquatic Plants. By Norman C. Fassett. (Revision Appendix by Eugene C. Ogden.) 405 pages. The University of Wisconsin Press, Madison, Wisconsin. 1957. $6.50.

This type of revision is rather unique as it offers the reader the opportunity to compare in the same book the original work with the revised presentation.

Dr. E. C. Ogden, State Botanist, New York State Museum and Science Service, was invited by the late Dr. Fassett to prepare the revision. The two men never had the opportunity to work together, and suggestions by correspondence were of a general nature. Dr. Ogden attempted to follow Fassett's wishes and was guided by his publications; however, final decisions were his own, for which he accepts responsibility.

The Revision Appendix is a revision of pages 3–341 of the 1940 first edition. The primary purpose is to bring the nomenclature into agreement with Fernald's revision of GRAY'S MANUAL, Gleason's revision of the BRITTON AND BROWN ILLUSTRATED FLORA, Muenscher's AQUATIC PLANTS OF THE UNITED STATES, recent local floras, and monographic treatments, including some by Fassett.

Important range extensions within the manual area have been added. Text and appendix have been newly indexed.

Dr. Ogden includes several keys in the Revision Appendix. Some are considered by the new author as supplementary keys (e.g. *Potamogeton*), one of Dr. Ogden's specialties, while others are replacement keys (e.g. *Echinodorus* and *Boltonia*). Several

of the revised keys are very helpful with the identification of difficult taxa. The *Callitriche* key is taken from Fassett's 1951 monograph.

The Revision Appendix added by Dr. Ogden enhances the value of a very useful book on the taxonomy of aquatic plants.—DAVID E. FAIRBROTHERS, Department of Botany, Rutgers, The State University, New Brunswick, N. J.

Spring Flora of Wisconsin. By Norman C. Fassett. (Third edition with revisions by Margaret S. Bergseng.) 189 pages. 29 pages of plates. The University of Wisconsin Press, Madison, Wisconsin. 1957. $2.50.

This is a pocket-sized field manual of plants growing in Wisconsin without cultivation and flowering before June 15.

Dr. Fassett had revised 57 pages of this book before his death, and subsequently several of his colleagues completed the project. Margaret S. Bergseng, an associate and former student, was responsible for most of the revisionary work.

The new edition includes increased botanical facts known about certain taxa and additional distribution information within the state of Wisconsin. The nomenclature is in accordance with the eighth editon of GRAY'S MANUAL OF BOTANY.

The small book ($6\frac{3}{4} \times 4\frac{1}{2}$ inches) was originally published in 1931, with the second edition appearing in 1947. The text of the latest edition has been improved by five botanists. The flexible waterproof plastic binding will be appreciated by field enthusiasts.—DAVID E. FAIRBROTHERS, Department of Botany, Rutgers, The State University, New Brunswick, N. J.

Ferns of Liberia. By Winifred J. Harley. (Reprinted from Contributions from the Gray Herbarium of Harvard University, No. CLXXVII, 1955.)

Mrs. Winifred J. Harley lived at the Ganta Methodist Mission, Liberia, Africa. Liberal is tropical, within 8 degrees of the equator. Since 1675, numerous botanists made collections as transient visitors in the country. They suffered from tropical diseases. Several died with their work unfinished. Mrs. Harley lists all previous collections in her reprint and where they may be studied.

Living in the area, she used her unique opportunity to study ferns at all seasons, and made repeated collections at three widely separated stations, increasing the number of known ferns from 45 to 118.

Her work gives a detailed geographic discussion of the country. She concentrates on fern ecology of the different areas with careful descriptions for each fern environment. The species represented are mostly tropical, some restricted to Africa, others such as *Pteridium aquilinum*, with more general distribution.

One plate of maps of political and physical features, and a plate showing plant habit, pinna, and sorus of *Ctenopteris punctata* Ballard illustrate the work. The reprint should be valuable to taxonomists, ecologists, and those studying physical and migrational relationships.—CLARA S. HIRES, Mistaire Laboratories, 152 Glen Avenue, Millburn, New Jersey.

A Field Guide to the Ferns. By Boughton Cobb, Houghton Mifflin Co., Boston, 1956, $3.75.

Mr. Cobb's book is a handy pocket-size companion for nature walks or field trips. This most recent of the Peterson Field Guide Series has a greater scope and many improvements over others of similar purpose. It includes not only ferns and fern allies of Northeast and Central U.S.A., but also a section on species of the British Isles and Western Europe. Many of these are similar to species found in this country.

Each fern is described and illustrated. As Dr. Wherry wrote, Laura Louise Foster's drawings for each fern are "among the best ever published, beautifully designed and exquisitely executed."

The book arrangement is convenient and efficient for instant reference. The illustrated descriptive keys are original, unconventional in their groupings but practical for dealing with large, easily recognized characters. The words used are simple, nontechnical, easily understood, and found elsewhere in similar good fern literature.

Each plant is described briefly under separate headings, such as leaves, leaflets, subleaflets, stalks, fruit dots, and fiddleheads. Pictures are labeled to explain these characteristics more clearly.

Several friends have exclaimed that they liked the book. They found it more convenient for beginners than books through which they had struggled, using a botanical dictionary and the author's glossary to interpret word meanings.

This book should widen the field of fern enthusiasts, as well as inspire and stimulate many amateurs to build their own fern library.—CLARA S. HIRES, Mistaire Laboratories, Millburn, New Jersey.

Ferns of the Ottawa District. By W. J. Cody. Canada Department of Agriculture. 1956, $1.00.

The book covers a 30-mile radius of Ottawa, including about 2800 square miles. The species are also of wide distribution throughout Northeastern America. A few are rare in the vicinity, and as Mr. Cody says, "probably at the northern limit of their range." *Dryopteris filix-mas* and *D. fragrans* are not found, but an excellent section of 17 pages on *Botrychium*, both common and rare varieties, is of real value.

Group collections were made chiefly by members of the Botany and Plant Pathology Division, Canada Department of Agriculture, and their herbarium formed the basis for the manual. Other organizations and individuals were recognized.

As mentioned in Mr. Cody's introduction, all known information was organized for the first time with keys and descriptions. Concise notes include habitats, collection dates, abundance and economic importance. Each of the 41 species is illustrated with a photograph of an herbarium specimen; and 40 maps pinpoint localities where each was collected.

Simplicity of presentation makes the book easily used by both laymen and scientists and fills a definite need.—CLARA S. HIRES, Mistaire Laboratories, Millburn, New Jersey.

Encyclopedia of Roses and Rose Culture. Edited by Harcourt P. Champneys and Carl Withner. 226 pages plus 9 color plates plus 65 halftones (32 pages) plus line drawings. First published by C. Arthur Pearson, Great Britain. Prentice-Hall, Inc., Englewood Cliffs, N.J. 1957. (revised). $7.50.

The earnest gardener will find here an excellent source for the answers to rose culture. Areas covered include the history, planning and choice of sites, classification, purchase, soils, construction, general culture and care, diseases and pests, exhibition, and a general glossary of the better varieties. Revision of recommended lists of various growth types and the glossary is especially recent and useful to the newest amateur horticulturist. Both beginner and experienced will find the guides to general culture and care authoritative and complete. Further revision, however, would be more valuable in at least two instances.

The editors deem it unfortunate that one should place roses in any but a primary position in the landscape. Modern practices and desires seek integration in the architecture of plantings. It would be most valuable to find a chapter dealing with the incorporation of roses into the general scheme. This same conservatism invades the descriptions of desirable arches, screens, and pergolas. Bed plannings are also in line with the formality of the traditional English garden.

The Encyclopedia will be an oft sought reference for the care of the two or three dozen roses under this reader's hand. He would appreciate more color photographs to aid in the choice of future resident varieties, especially at the price quoted.—JOHN J. NELSON, New Brunswick Senior High School, New Brunswick, N. J.

Botany: An Introduction to Plant Science. 2nd edition. By Wilfred W. Robbins, T. Elliot Weier, and C. Ralph Stocking. 589 pages. John Wiley & Sons, Inc., New York, N.Y. 1957. $6.95.

The second edition is in many ways superior to the first. Not only have the authors brought certain phases of botany up to date, but they have reorganized several chapters in an effort to place more emphasis upon the organism as a functioning unit. In this reorganization, fragmentary discussions on physiology in chapters of the first edition entitled "The Root", "The Stem", "The Leaf", and "The Plant as a Living Organism" were combined in the second edition into chapters called "Soil and Mineral Nutrition", "Transpiration, Conduction, and Absorption", and "Photosynthesis and Respiration", thus leaving the former chapters to descriptive discussions and general functions.

Other noteworthy revisions include more emphasis on the life cycle of angiosperms and comparisons with the life cycles of primitive forms, a new chapter devoted to descriptions of certain angiosperm families which illustrate the Besseyan system of classification, addition of a discussion on *Chlamydomonas*, and a glossary. Each chapter has had some rewriting but those on stem, leaf, and flower have been noticeably supplemented.

The book can be summarized as follows: introduction, a brief chapter on ecology in the form of a discussion on major plant formations, classification, gross morphology, cell, stem, root, leaf, physiology, flower, seed, seedling, and inheritance. The interrelationships of these are then expressed in a chapter entitled "The Plant as a Living Organism" in which plant behavior is discussed on the basis of effects of environmental and hereditary factors on internal processes. After this come eleven chapters devoted to major plant groups in which the salient features and possible evolutionary position of each are discussed.

The book is well written, organized, illustrated, and indexed. These qualities should make it a useful text for beginning courses as well as an excellent reference source for instructors.—Carl D. Monk, Department of Botany, Rutgers, The State University of New Jersey, New Brunswick, New Jersey.

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INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF BRITTONIA

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